is the utricle, form two sacs which are filled with endolymph communicating through a narrow canal. (Fig. 8.) From the mid-point of this canal, and forming a V-shaped juncture with it, is a third canal by which both communicate with a lymphatic sac beneath the dura mater. The duct is called the endolymphatic duct, and the sac the subdural endolymphatic sac. The scala tympanum communicates by a small duct with the saccule. (Figs. 9 and 10.)

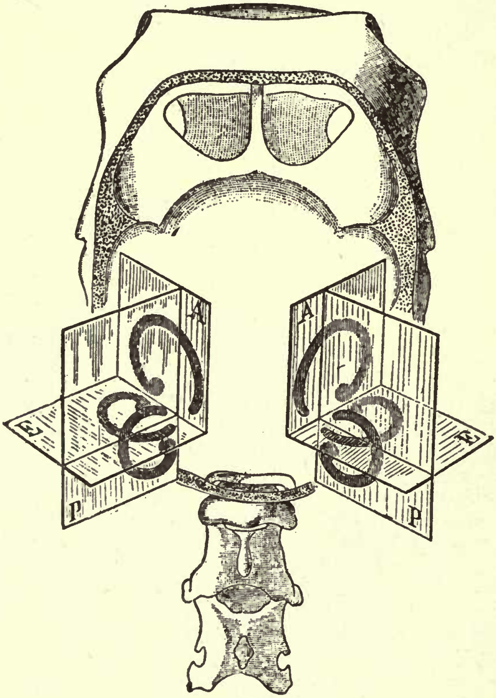

Fig. 11.—Figure from Ewald, Showing the Situation of the Three Semicircular Canals in the Skull of the Pigeon (Starling).

It should also be mentioned that the scala tympanum communicates with the subdural space by a small duct or canal, the aqueductus vestibuli.

Beginning and ending in the utricle are three semicircular canals. They form almost a complete ring and occupy the three planes of space. (Fig. 11.) One end of each semicircular canal is enlarged in a fusiform manner. This enlargement is called the


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LECTURE NOTES ON PHYSIOLOGY

BY

HENRY H. JANEWAY, M.D.

THE SPECIAL SENSES

NEW YORK
PAUL B. HOEBER
67-69 EAST 59TH STREET

THE SPECIAL SENSES

HEARING

SOUND

Auditory Stimuli—By means of the auditory apparatus we are informed of certain external changes which are capable of producing a wave-like vibration of the molecules of the air, occurring at smaller or longer distances from us and transmitted to us by the air. Such stimuli are called sound. The waves of air constituting sound strike against the drum of our ear and set in movement a delicate transmitting apparatus which causes the stimulus of each wave of the air to affect the terminations of the auditory nerve.

The delicacy of the apparatus is so great that not only is the existence of vibrations detected below the limits of 30 and 10,000 to 20,000 vibrations a second, but also up to 4,000 vibrations a second, the actual number of vibrations a second constituting pitch and all their modifications produced by accessory vibrations and manner in which sets of vibrations of the air forming a series of waves are repeated. When the vibrations constituting the waves of air are repeated in a very irregular manner a noise is produced more or less disagreeable to the mind. When the vibrations of the waves repeat each other with a more or less regular rhythm a musical tone is produced.

Qualities of Sound—Musical tones, and in certain particulars noises, may be varied in a number of different ways.

First, as to loudness. A louder tone is produced by increasing the amplitude of the vibrations. When the prongs of a tuning fork are made to vibrate through a greater distance the note is louder. The amplitude may be recorded on a moving blackened surface.

Second, as to pitch. The height of a note, that is its pitch, is determined by the number of vibrations a second. The pitch of one fork differs from that of another by vibrating at a different

rate. By means of a revolving siren the number of vibrations of any note may be ascertained.

No musical note is produced by vibrations of less frequency than 30 a second. The human ear will appreciate as a higher pitch an increasing number of vibrations each second up to 4,000 a second, beyond which no note at all is heard.

Third, as to timbre or quality. The note from a violin differs in quality from that of a piano or the human voice. In what does this difference consist? If a stretched wire be plucked so that it is set in vibration, it will not only vibrate as a whole, but portions of it, halves, thirds or fourths, will begin vibrating separately. Each separately vibrating portion will vibrate with that frequency which is inversely proportional to the fraction which the separately vibrating portion constitutes of the whole.

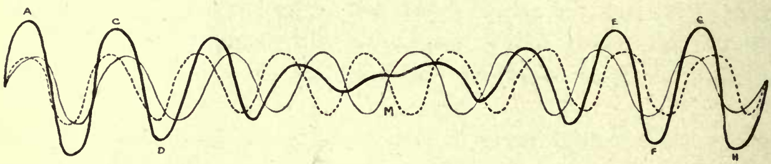


FIG. 1.—ILLUSTRATION OF THE REINFORCING AND NEUTRALIZING EFFECT OF TWO WAVES, POSSESSING A DIFFERENT FREQUENCY OF VIBRATION, UPON EACH OTHER.

At A and C the sound is maximum, approaching which there is a crescendo. At M the sound is lost and approaching it there is a descrescendo.

Thus one-third of the wire will be vibrating three times as frequently as the whole wire, and one-half of the wire twice as rapidly.

Every unit of a musical instrument, in addition to its fundamental note, gives out overtones or harmonies which vibrate in ratios of a numerical progression, or 1, 2, 3, 4, 5, 6, etc., with the fundamental note.

The number and varying prominence of the various overtones determine quality. The tuning fork is the only known instrument practically free from overtones. This makes it such a valuable tuning instrument.

All these single vibrations come to the ear combined together in a compound wave. This compound wave may be analyzed by bringing resonators near the source of its production. Each

resonator vibrates with a frequency of its own and each resonator will be set vibrating by the vibrations coming from the overtones vibrating with the same frequency. When two musical notes are sounded together the frequency of both their fundamental notes and overtones will differ. This difference will cause the waves of air to pass along together in different phases so that at certain intervals the waves from both instruments will coincide and accentuate each other, while at other intervals they will interfere and diminish the loudness of the sound of each. (Figs. 1 and 2.)

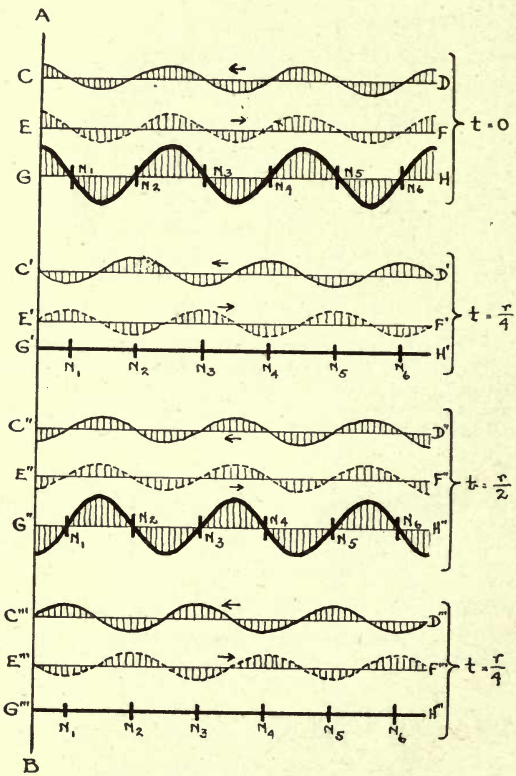


FIG. 2.—DIAGRAM ILLUSTRATING THE REINFORCING AND NEUTRALIZING EFFECT OF WAVES IN THE SAME AND OPPOSITE PHASES UPON EACH OTHER.

The line A B may be considered a section of a vertical wall against which the waves D C and F E, D′ C′ and F′ E′, D″ C″ and F″ E″, D‴ C‴ and F‴ E‴ strike. The heavy lines H G and H″ G″ illustrate the reinforcing effect of waves in the same phase, and the heavy lines H′ G′ and H‴ G‴ represent the neutralizing effect of waves in opposite phase.

An alternately occurring waxing and waning of the sound is known as beats. The number of beats in each second may be used to determine the difference in the vibration frequency of two forks vibrating together. It is quite clear that if there are ten beats a second and one fork is vibrating 100 times a second, the other must be vibrating 110 times a second, because after each interval of ten vibrations the forks will be in opposite phases of vibration.

As the number of beats increases, the effect becomes more and more disagreeable to the ear, just as a light frequently flickered in front of the eye becomes disagreeable. When the beats reach 33 times a second the effect is most disagreeable. Beyond this they are not distinguished, but we speak of the phenomenon as discordant.

The opposite of dissonance is consonance. It involves, in the first place, an absence of too pronounced and too frequent beats, and such a reinforcement of the amplitude of the main or fundamental tone and of the overtones as will create a regular amplitude or rhythm. In the beat consonance or harmony there is a complete agreement of the two notes, at least in their fundamental tones and the greater number of their overtones. A nearly complete harmony is illustrated when the same notes of different octaves are sounded together.

Musical Notes—The repetitions together of certain other notes are recognized in music as harmonious or pleasant, because there is sufficient agreement between them not to be disagreeable and enough variations not to be monotonous.

They are notes differing in their number of vibrations in the following ratio:

C 1:2 equals an octave
G 2:3 equals a fifth
F 3:4 equals a fourth
E 4:5 equals major third
O 5:6 equals minor third
B 5:8 equals minor sixth
A 3:5 equals major sixth

If we should write out these fundamental tones with their overtones increasing in these ratios, it will be easy to see the

frequency of consonance and therefore the degree of harmony between them. The heavy numbers mark the consonant notes:

Octave 1:2—	1	2	3	4	5	6	7	8	9	10
C		**2**		**4**		**6**		**8**		**10**
Fifth 2:3—	2	4	6	6	8	10	12	14	16	18
G	3		**6**		9		**12**	15		**18**
Fourth 3:4—	3	6	8	12	15	18	21	24	27	30
	4	8		**12**		20		**24**	28	
Major third 4:5—	4	8	12	16	20	24	28	32	36	40
E	5		10	15	**20**	25	30	35		**40**
Minor third 5:6—	5	10	15	20	25	30	35	40	45	50
	5	12	18	24		**30**	36	42	48	
Major sixth 3:5—	3	6	9	12	15	18	21	24	27	30
	5		10		**15**	20		25		**30**
Second 8:9—	8	16	24	32	40	48	56	64	72	
D	9	18	27	36	45	54	63		**72**	

Seventh 8:5—Concordant at 8th overtone.
B

The vibration frequency of the various notes used in music differ from each other in the ratio of the above table.

C—Possesses a vibration frequency in the different octaves of 33 and its multiples, each higher octave representing double the number of vibrations of the last, thus: 33, 66, 132, 264, 528, 1056 and 2112.

D—A vibration frequency of 37.125 and its multiples, thus 37.125, 74.25, 148.5, 297, 594, 1188, 2376.

E—41.25 and similar multiples.

F—44, etc.

G—49.5, etc.

A—55, etc.

B—61.875, etc.

The C major scale is therefore:

C. C:C equals octave 33:66 equals 1:2.

D. C:D Second equals 33:37.125 equals 8:9.

E. C:E equals major third 33:41.25 equals 4:5.

F. C : F Fourth 33 : 44 equals 3 : 4.

G. C : G equals fifth 33 :49 : 5 equals 2 : 3.

A. C : A equals sixth 33 : 55 equals 3 : 5.

B. C : B equals seventh 33 : 61.875 equals 8 : 15.

The major chord with C as the fundamental tone is C.E.G. with a vibration frequency of 1, 5 and 3, i.e., 4, 5, 6. The same ratio, 5 : 4 and 3 : 2, will obtain between the notes of the major cord if G or F is taken as the fundamental tone.

When two tuning forks are sounded together with a proper interval (say 1/5) between them a combination tone may result. The combined tone may either correspond in vibration frequency to the difference between the two fundamental tones, and thus produce a note an octave below the pitch of the lower pitched fork, or to the sum of vibrations of the two forks. In any case the phenomenon is objective, not subjective.

The human ear is capable of analyzing all these differences in vibration frequency of compound tones. An individual with a trained ear can not only tell the difference between the various combinations of overtones which make one instrument differ from another, but can even name the chord and notes composing it when it is sounded on any musical instrument.

How, then, is this intricate analysis accomplished? What is the delicate mechanism which is capable of transmitting the separate elements of compound waves of music or other sounds to the mind?

THE EAR

The Anatomy of the Ear—The human ear consists of an external, a middle and an internal portion. The external portion is roughly funnel-shaped and placed on the side of the head. Its sole function is to gather the waves of air, concentrating them, so to speak, upon the tympanic membrane. From the external ear a canal leads internally from the cone-shaped internal end of the funnel. This is called the external auditory meatus. Its inner end is closed by a thin membrane called the drum-head or the tympanic membrane. (Fig. 3.)

The walls of the canal secrete a wax-like material called cerumen, which together with hairs prevents dust and insects and other beasts from entering the ear.

Every vibration of the air striking the tympanic membrane sets it into vibration with an amplitude and frequency of variations which correspond precisely to the character of the wave striking it.

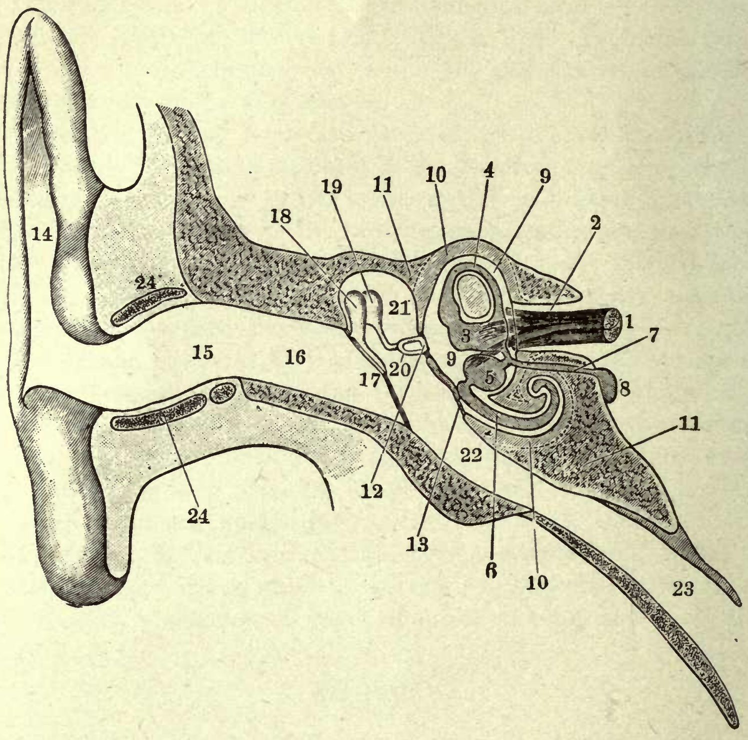


Fig. 3.—Schematic Representation of the Relations of the Various Portions of the Ear.

1, the vestibular and auditory nerve entering the internal auditory meatus to be distributed to the various portions of the internal ear; 3, utricle; 5, saccule; 6, cochlea; 7, ductus endolymphaticus; 8, its terminal cul-de-sac, or the saccus endolymphaticus; 9, perilymphatic space; 10, walls of the bony labyrinth; 12, fenestra ovalis; 13, fenestra rotunda; 14, external ear; 15 and 16, external auditory meatus; 17, lymphatic membrane; 18, malleus; 19, incus; 20, stapes; 22-23 indicates the Eustachian tube.

No matter how complex this may be, the movement of the tympanic membrane reproduces all the elements in the sound waves striking it. This movement is transmitted across a small cavity termed the middle ear, or tympanum, by a chain of three little

bones, the ossicles of the middle ear. The transmission by these bones diminishes the extent of the movement of the tympanic membrane, but proportionally intensifies it.

The malleus is attached to the tympanic membrane by its long process, which moves, therefore, with the membrane. The head of the malleus articulates with the incus, the second bone in the chain of ossicles. The incus also has a long process which articulates by its tip with the stapes. The articulations of the incus with the malleus and stapes is so arranged that every time the long process of the incus moves inward the stapes move inward, but the axis of rotation of the incus is so placed that its long process forms the shorter arm of the lever in the proportion of 2 : 3. Inasmuch as the tympanic membrane is 20 times as big as the fenestra ovalis, into which the stapes fits, the movements of the former are 20 times as great. Consequently the amplitude of the movements of the stapes will be 2/3 by 1/20 or 1/30 of the movement of the tympanic membrane, but thirty times as intense. Provision also exists for stretching the tympanic membrane by means of a little muscle, the tensor tympani. This muscle contracts whenever sound falls on the ear. Moreover, the muscles of both sides contract even though the sound falls on one ear alone. The tympanic membrane bulges outward, and so, when the tensor tympani controls it, relaxes the tympanic membrane.

The amplitude of an aerial particle in a sound wave just within the limits of audibility is only 1/1,000,000 of a mm. The longest sound waves which are audible are .0004 mm., which is equal to 0.1 the length of a wave of green light. The energy perceived in light and sound are of the same order of magnitude. The most internal of the three ossicles, the stapes, is attached to a small membrane which separates in part the internal ear from the middle ear. This membrane is a very small one and simply closes a window in the inner wall of the internal ear. Immediately below this window is another window closed by a membrane which also serves to separate the internal from the middle ear. The middle ear is a cavity containing air. The internal ear, on the other hand, is a bony cavity lined with a delicate membrane which is filled with fluid. The movements of the most internal ossicle, the stapes, are transmitted to the lymph filling the internal ear. This lymph, inclosed within a bony cavity, cannot be set in motion unless the second

window already mentioned below the stapes exists to permit of displacement of the lymph each time it is pressed upon by the movements of the stapes. This second window is called the fenestra rotunda. To make a long story short, the waves of air are transformed into currents in the fluid of the internal ear which duplicates every detail of the waves of the air. Every time the stapes move inward the second window, the fenestra rotunda, below it, moves outwards and vice versa. (Fig. 4.) The movement of this

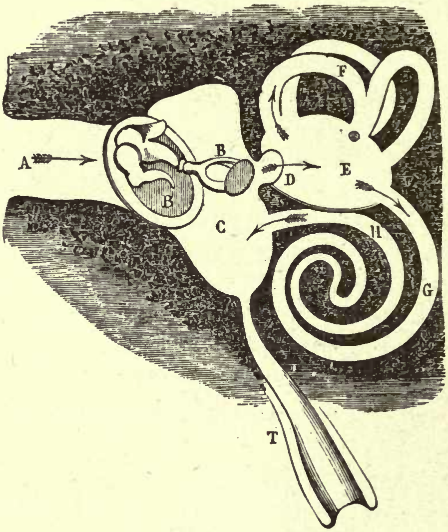


Fig. 4.—Schematic Figure Showing the Direction and Method of Transmission of the Sound Vibrations.

A, waves of air striking the drum head; B, chain of ossicles transmitting the sound vibrations across the tympanum or middle ear to the fenestra ovalis, D, from which the vibrations are imparted to the lymph in the vestibule, E, and thence to the lymph in the scola vestibule, G, returning through the scola tympani, H, to end at the fenestra rotunda.

lymph is further facilitated by the shape of the passages in forming the internal ear within which it is contained.

Immediately internal to the cavity of the tympanum, from which it is separated in part by the two windows just mentioned, is the cavity of the vestibule. This is rather a large space containing two sacs, the utricle and saccule, and the beginning of the first turn of a cone-shaped structure, the cochlea. The cochlea consists of a central stem, the modiolus. Around the modiolus are wound in

two and one-half turns two spiral canals which are separated from each other by a bony crest projecting from the modiolus between the spiral canals for their whole length. The upper of these two canals is called the scala vestibuli and the lower the scala tympani. (Fig. 5.)

These canals do not completely divide the cochlea into the two longitudinal portions. The division is completed by two membranes which reach from this margin of the crest to the opposite wall of the cochlea. These two membranes inclose between them a third canal, triangular on cross-section and called the scala media. At the apex of the cochlea (the helicotrema) the scala vestibuli and

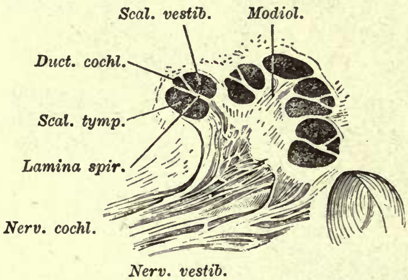


Fig. 5.—Cross Section of the Cochlea in a Plane to Show Its Long Diameter.

scala tympani communicate with each other. A wave of lymph, or in this situation endolymph, started in the scala vestibuli, would therefore pass the whole length of the scala vestibuli and return through the scala tympani. As this wave passes it produces an undulation of the membranous roof of the scala media.

The fenestra ovalis, which is closed by the stapes, separates the cavity of the middle ear from the vestibule, so that the movements of the membrane over the fenestra ovalis produced by the movements of the stapes are transmitted first to the fluid within the vestibule. The movement in this fluid starts the movement of the fluid wave in the scala vestibuli which opens into the cavity of the vestibule. The return wave through the scala tympani is received by the membrane covering the fenestra rotunda, the second window, which separates the middle ear from the internal ear.

The scala tympani ends abruptly against this membrane, which may be viewed as closing its external termination. The membrane

of the fenestra rotunda, therefore, separates the middle ear cavity from the scala tympani rather than from the vestibule, although the scala tympani communicates with the vestibule. The movements of the membrane of the fenestra rotunda will therefore be in an opposite direction to those of the fenestra ovalis. The scala media, as has been said, is formed by two membranes passing from

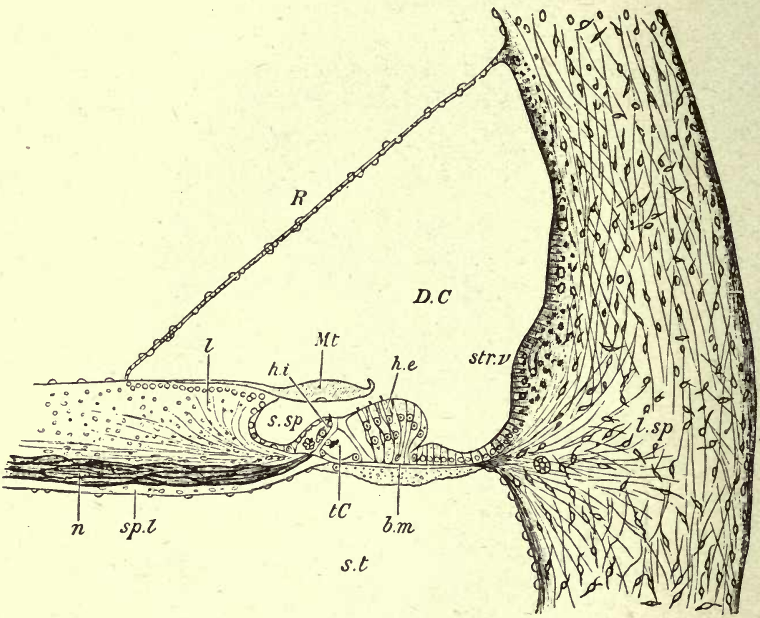


Fig. 6.—Vertical Section of the First Turn of the Human Cochlea. (G. Retzius, Starling.)

s. v., scala vestibuli; *s. t.*, scala tympani; *d. c.*, canal or duct of the cochlea; *sp. l.*, spiral lamina; *n.*, nerve fibers; *l. sp.*, spiral ligament; *str. v.*, stria vascularis; *s. sp.*, spiral sulcus; *R*, section of Reissner's membrane; *l*, limbus, laminæ spiralis; *m. t.*, membrana tectoria; *tC*, tunnel of Corti; *b. m.*, basilar membrane; *h. i. h. e.*, internal and external hair-cells.

the free edge of the spiral crest which serves to separate the scala vestibuli from the scala tympani to the outer wall of the cochlea.

The lower of these two membranes passes directly across from the edge of the spiral crest to the outer wall of the cochlea. It is called the basilar membrane and is composed of strong elastic fibers. It separates the scala media from the scala tympani below and is strong and resistant. The width of this membrane, in other

words, the length of its fibers, increases from .041 mm. at the base of the cochlea to .495 mm. at the helicotrema.

The auditory epithelium is situated upon the upper surface of this membrane. The roof of the scala media is formed by a very thin delicate membrane, the membrane of Reissner, which separates the scala media from the scala vestibuli and passes from the edge of the spiral crest upwards and outwards to the outer wall of the cochlea. A cross-section of the scala media would present roughly a right-angle triangle with the right angle between the basilar membranes and the outer wall of the cochlea.

The auditory epithelium containing the sensitive elements, which transform the waves in the endolymph into nervous im-

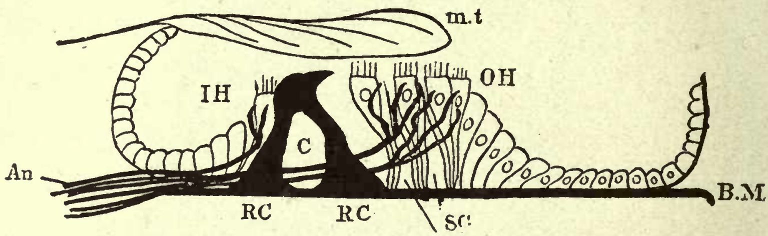


FIG. 7.—SECTION THROUGH THE END-ORGAN OF THE AUDITORY NERVE IN THE COCHLEA (ORGAN OF CORTI).

B.M, basilar membrane; C, canal of Corti; RC, rods of Corti; IH and OH, inner and outer hair cells; SC, sustentacular cells; *An*, auditory nerve; *m.t*, membrane tectoria (Starling).

pulses, is called the organ of Corti. It consists of a double row of stiff cells, the rods of Corti, enclosing a canal, the canal of Corti, between them. This canal is placed upon the upper surface of the basilar membrane at its junction with the spiral crest and passes the whole length of the scala media. On the two sides of the rods of Corti are the auditory epithelial cells; on the inside a single row of cylindrical epithelial cells possessing hairs projecting from their free surface, and on the outside three rows of similar hair cells. (Figs. 6 and 7.)

The cells are supported by other epithelial cells called sustentacular cells, or cells of Deiters, which are placed between the bases of the hair cells. The cells of Deiters join each other at the free margin of the hair cells in such a manner that they form a very delicate membrane possessing holes, through which the hairs

of the hair cells project. This delicate membrane is called the membrana reticularis. Projecting over the hairs and the membrana reticularis from the free edge of the spiral crest is another membrane unattached at its opposite margin and resting on the membrana reticularis. It is called the membrana tectoria and may be conceived of as forming a damper to the action of the waves of fluid as they pass over the hair cells.

Physical Basis of Hearing—The complex structure of this organ of hearing suggests with a force which amounts to demonstration that the power of the human being to analyze sound depends upon the structure of this peripheral organ. The different length of the fibers of the basilar membrane upon which the organ of Corti rests indicates that these fibers, like resonators, vibrate only to waves adapted to the vibratory frequency of each fiber, the fibers varying in length from 135 micro mm. at the base of the cochlea to 234 micro mm. at the apex, and the whole structure containing about 24,000 fibers.

At least 4,500 such resonators are necessary in order to enable us to distinguish notes varying from 30 to 4,000 vibrations per second. In the middle of the scale, however, we can distinguish notes differing only by .3 to .5 vibrations per second. The varying length of the fibers of the basilar membrane would account for this number of resonators and such a selective stimulation of the hair cells.

We recognize a note then because the wave of endolymph causes only a certain fiber to vibrate. This vibrating fiber causes the hair cells upon it to rise and fall and their hairs to come into contact with the membrana tectoria.

Certain facts support this view. If the ear has become fatigued to a note with a vibration frequency of 160 so that it does not hear it so intensely, and then is allowed to listen to another note with a vibration frequency of 165, all evidence of fatigue will have disappeared. This fact indicates that other hair cells with other central connections have been stimulated. In the same way disease in man in which the base of the cochlea has alone been injured has caused a loss of perception to only the high notes.

Similar confirmatory experiments have been tried successfully on animals: i.e., injury to one or the other end of the cochlea has caused loss of perception to high or low notes.

The Distribution of the Auditory Nerve—The auditory nerve enters the central canal of the modiolus and distributes its branches in a fan-shaped manner between the layers of bone forming the spiral crest which separates the scala vestibuli from the scala tympani. Each fiber as it lies between the layers of the crest passes through a bipolar cell. These cells retain their true embryological bipolar character.

The Anatomy of the Vestibule and Semicircular Canals—The above description only deals with half of the internal ear. The

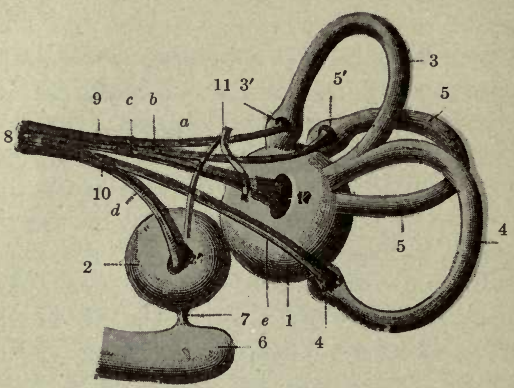


FIG. 8.—THE UTRICLE, SACCULE AND THE SEMICIRCULAR CANALS SEEN FROM THEIR INTERNAL SURFACE AND SHOWING THE OPENINGS FOR THE VESTIBULAR NERVES.

1, vestibular pocket; 2, saccule opening, with 2′, its vestibular opening; 3, 4, 5, superior, posterior and external semicircular canals. with 3′, 4′, 5′, their vestibular openings; 6, canal of the cochlea; 7, canal of Hensen; 8, vestibular branch of the eighth cranial nerve; 9, its superior branch with, *a*, nerve to the superior ampule, *b*, nerve to the external ampule, *c*, the utricular nerve; 10, inferior vestibular branch, *d*, saccular nerve, *e*, nerve to the posterior ampule; 11, endolymphatic canal.

other half, though called a part of the internal ear, has nothing whatever to do with hearing. It is, however, inclosed in the same bony cavity. Its function is solely limited to the sense of equilibrium. We must, therefore, never forget that the internal ear is a double organ.

The portion furnishing the brain with sensations of equilibrium includes the saccule and utricle contained within the cavity of the vestibule and the semicircular canals which communicate with the cavity of the vestibule. The saccule and utricle, of which the larger

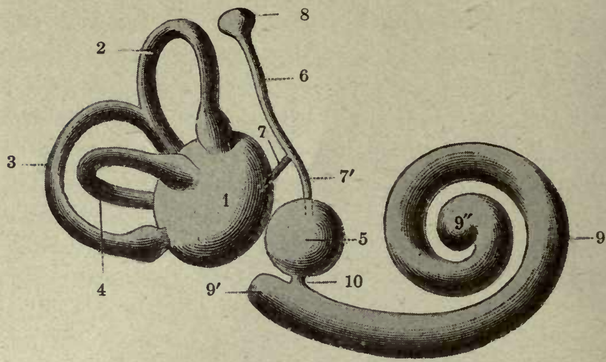


FIG. 9.—MEMBRANOUS LABYRINTH OF THE RIGHT SIDE, SEEN FROM THE EXTERNAL SURFACE.

1, utricle; 2, superior semicircular canal; 3, posterior semicircular canal; 4, external semicircular canal; 5, saccule; 6, endolymphatic canal, with 7 and 7′, its two branches, and 8, its vestibular cul-de-sac; 9, cochlear canal, with 9′, its vestibular, and 9″, its terminal cul-de-sac; 10, canalis reuniens of Hensen.

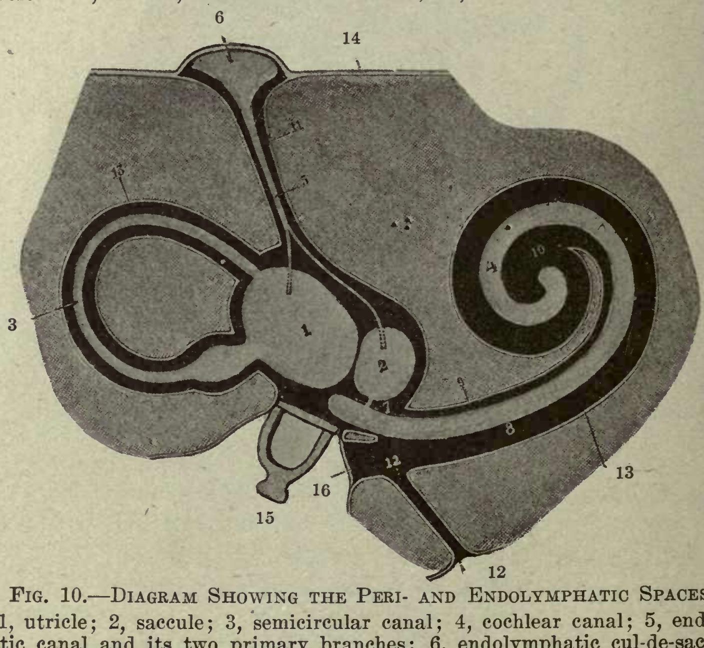


FIG. 10.—DIAGRAM SHOWING THE PERI- AND ENDOLYMPHATIC SPACES.

1, utricle; 2, saccule; 3, semicircular canal; 4, cochlear canal; 5, endolymphatic canal and its two primary branches; 6, endolymphatic cul-de-sac, covered by the dura mater; 7, canal of Hensen, uniting the saccule and the vestibular portion of the cochlear canal; 8, scala tympani; 9, scala vestibuli; 10, communication of the two scalæ at the helicotrema; 11, aqueductus vestibuli; 12, aqueductus tympanum; 13, periosteum; 14, dura mater; 15, stapes in the fenestra ovale; 16, fenestra rotundum.

is the utricle, form two sacs which are filled with endolymph communicating through a narrow canal. (Fig. 8.) From the mid-point of this canal, and forming a V-shaped juncture with it, is a third canal by which both communicate with a lymphatic sac beneath the dura mater. The duct is called the endolymphatic duct, and the sac the subdural endolymphatic sac. The scala tympanum communicates by a small duct with the saccule. (Figs. 9 and 10.)

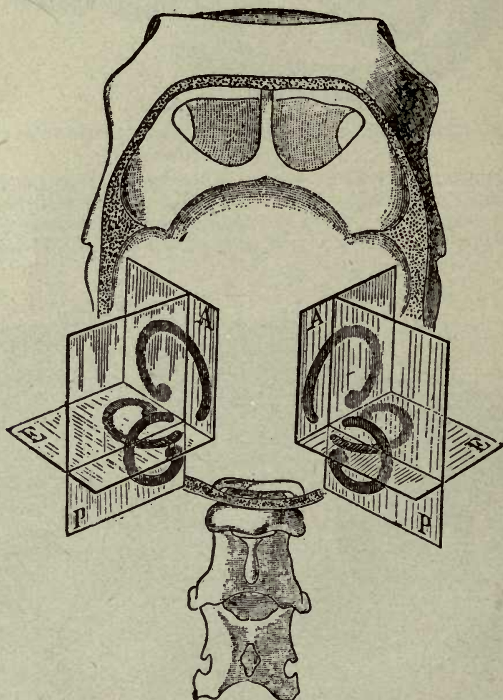


FIG. 11.—FIGURE FROM EWALD, SHOWING THE SITUATION OF THE THREE SEMICIRCULAR CANALS IN THE SKULL OF THE PIGEON (STARLING).

It should also be mentioned that the scala tympanum communicates with the subdural space by a small duct or canal, the aqueductus vestibuli.

Beginning and ending in the utricle are three semicircular canals. They form almost a complete ring and occupy the three planes of space. (Fig. 11.) One end of each semicircular canal is enlarged in a fusiform manner. This enlargement is called the

ampulla and in each canal it is placed near the utricle. (Figs. 11, 12.)

The epithelium, along a line on the concave side of each semicircular canal, is raised in a ridge in a manner to expose it to currents of lymph through the canal. At an elevation in the saccule and utricle the epithelial cells are higher and possess hairs protruding from their free surface.

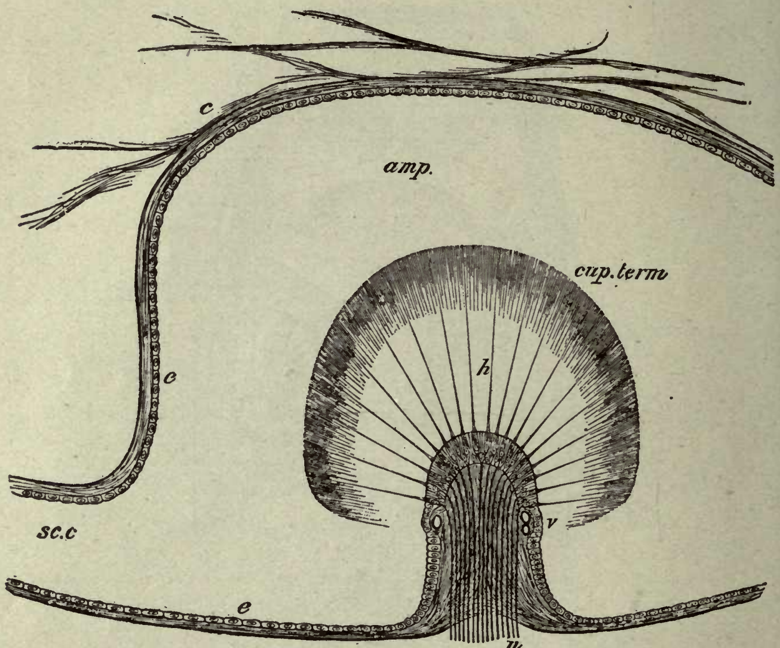


FIG. 12.—END-ORGAN OF THE VESTIBULAR NERVE IN AMPULLA OF SEMICIRCULAR CANAL ("CRISTA ACUSTICA"). (STARLING.)

Among these hairs are embedded calcareous concretions called otoliths, which are protected in their position among the hairs by an overhanging membrane, the otolithic membrane.

These areas of hair cells in the saccule and utricle are called maculæ acusticæ. In the ampulla of each semicircular canal is an elevation of cells possessing hairs and resembling in every way those of the macula acustica of the saccule and utricle. The hair cells in the semicircular canals are continuous with the high cylin-

drical cells of the concave surface of the semicircular canal and form with them the semilunar fold.

The area of hair cells in each ampulla is called the crista acustica. Any change in the position of an individual will cause a flow of fluid through the semicircular canals in the opposite direction to the movement. The flow will be most rapid in that semicircular canal which corresponds to the plane of the movement. It will flow over the hairs of the cells of the cristæ acusticæ and in this manner stimulate them proportionally to the degree and direction of the movement of the body. Any change of position in an individual also produces a change in the position of the calcareous particles in contact with the hair cells of the maculæ acusticæ. Removal of individual canals in pigeons causes abnormalities of position referable to particular planes of space (see Fig. 13). All these sensory areas are richly supplied by the terminal branches of the vestibular nerve which forms such important connections in the medulla and with the cerebellum and by means of the posterior longitudinal bundle are connected with other cranial nerves. The ganglion of this nerve is situated in the internal auditory meatus. Its cells retain their original bipolar character.

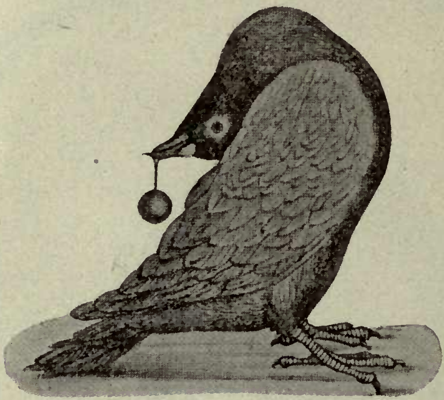


FIG. 13.—ILLUSTRATING THE POSITION TO WHICH THE PIGEON ALWAYS TURNS ITS HEAD AFTER BLOWING IN THE SAME DIRECTION OVER THE EXPOSED AMPULLÆ OF ITS SEMICIRCULAR CANALS.

VISION

The sensory organ for sight must not only be furnished with a sensitive surface capable of transforming light stimuli into nerve impulses with proper central endings, but also with some mechanism which is capable of causing the rays of light coming from external objects to fall on that surface, recombined in a manner to reproduce the exact counterpart respecting relative position and varying degrees of light and shade and color of all points of objects looked at. We speak of this as the reproduction of the image of external objects upon the surface of the eye. It is precisely the same sort of image as is reproduced upon the ground glass of the camera.

The sensory surface of the eye is called the retina.

The mechanism for the reproduction of images of external objects is called the dioptric mechanism.

The Dioptric Mechanism—The dioptric mechanism consists of three refractive surfaces and two fluid media.

A beam of light in passing from the external world to the retina must traverse these three surfaces and two media, all of which will change its course. The change in its course is of such a character that the rays coming from any one point in the external world looked at by a normal eye reunite again in the retina. It is possible, therefore, to determine what we may term a mean refractive surface, so that all the rays of light may be viewed as passing through a single surface and brought to focus by a single change in direction.

The refracting surfaces and media of the eye from without inwards are as follows:

1. Cornea, the glassy portion of an eye.
2. The aqueous humor, the fluid filling the anterior and posterior chambers of the eye. These chambers, separated by the iris or diaphragm of the eye, occupy the space between the cornea and the lens.
3. The anterior surface of the lens.
4. The posterior surface of the lens.
5. The vitreous humor, a jelly-like semi-fluid substance occupying the space between the lens and the retina. The refractive index of the vitreous humor is the same as that of the aqueous

humor, so that practically the eye may be considered as possessing only one refracting fluid.

The Nodal Point—If we determine the position and degree of curvature of a hypothetical refractile surface, capable of reuniting all the rays of light in the manner accomplished by the three refractive surfaces and two refractive media of the eye, it will lie within the anterior chamber of the eye, 2.3 mm. behind the anterior surface of the cornea, and curved about a center situated 0.47 mm. in front of the posterior surface of the lens. This center is called the nodal point. The refractive index of a normal eye is such that all parallel rays of light are brought to a focus on the retina by this hypothetical refractile surface.

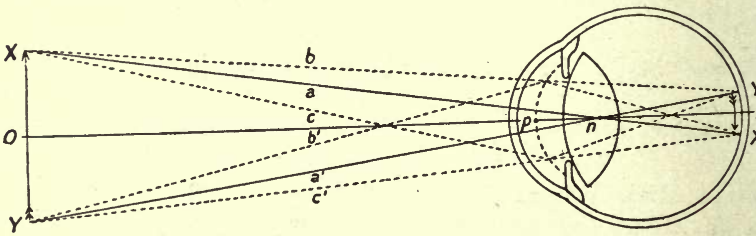


FIG. 14.—PATH OF THE RAYS IN THE FORMATION OF AN IMAGE ON THE RETINA (STARLING).

To reconstruct the path of rays of light through an eye, lines may be drawn from any two points of an external object through the nodal point to the retina. These rays are perpendicular to the hypothetical refracting surface and are not, therefore, refracted. All other rays from these same points are refracted to such a degree that they focus upon the retina at the same points where internal rays from these points of the external object strike the retina. (Fig. 14.)

The focal distance of the anterior surface of the cornea is 23 mm. Parallel rays of light on passing through it are brought to a focus at this distance from it. That of the whole eye is 15 mm., and that of the lens is 44 mm. It is quite clear, therefore, that the anterior surface of the cornea is the most important refracting surface of the eye.

Under water the curvature of the cornea is much flattened by the pressure of the water. Only near-sighted people can, there-

fore, see distinctly under water. All others become very far-sighted.

The image formed upon a retina is inverted and reduced in size. The angle formed by the rays of light passing from the extreme points of any external object through the nodal point of the eye is termed the visual angle. (Fig. 15.)

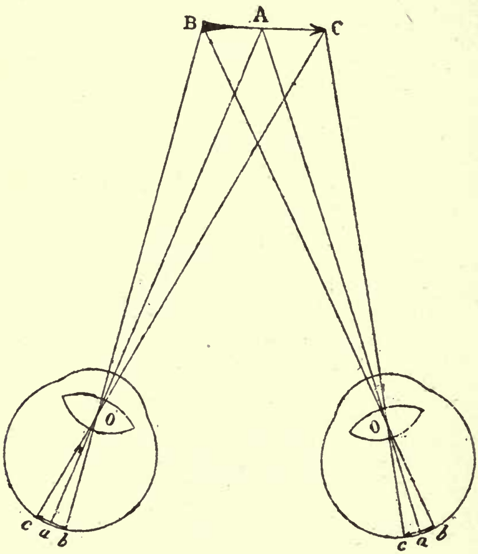


FIG. 15.

C O B, visual angle; c O b, the angle subtended by the image on the retina by the object, B C; O, the nodal point or optic center situated a short distance in front of the posterior surface of the lens; Aa Aa, optic axes; cb, reversed and reduced images of the object, B C.

Few individuals can distinguish two points as separate which subtend a smaller visual angle than 60 seconds. The angle represents a distance of .00438 mm. on the retina. This distance corresponds well with the distance between the elements in the retina which are responsible for distinct vision. In the central yellow spot of the retina vision is most acute. The visual elements here are alone the cones. They are .002 to .005 mm. thick. The cones are further separated from each other in the peripheral region of the retina where vision is less acute.

The Necessity for Accommodation—In the normal eye parallel

rays of light come to a focus on the retina, the eye being at rest. All rays coming to the eye from a distance further than twenty feet may be considered parallel. Rays of light coming to the eye from a near point will diverge as they approach the eye, and in order that they may be focused on the retina the curvature of the lens must be changed. It must be made more convex. There is not

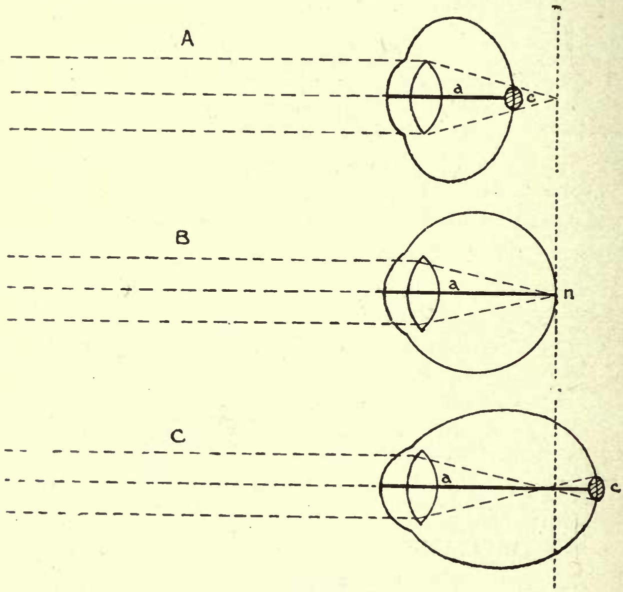


Fig. 16.—Schematic Representation of Refraction in the (A) Hypermetropic Eye, (B) Emmetropic Eye, and (C) Myopic Eye in Focal Point.

a, optic axis; *c*, diffusion circle on the retina produced by the failure of parallel rays to be focused upon it.

in all eyes a normal relation between the length of the eye and its refractive index. Deviations from the normal are possible in three directions:

Either parallel rays of light may be brought to a focus at a point in front of the retina or at a point behind the retina.

In the first case the anteroposterior diameter of the eye is too long for the refractive power of the cornea and lens of the eye. Such an eye is termed near-sighted, or myopic. When the reverse of this condition is present the eye is far-sighted, or hypermetropic. (Fig. 15.)

The third manner in which an eye may vary from the normal is in possessing a different refractive power in the horizontal and vertical meridian. Such a condition is called astigmatism. (Fig. 17.)

When present rays of light coming to the eye in the horizontal plane are focused upon a different anteroposterior plane than those coming to the eye in a vertical plane.

Sometimes the eye is hypermetropic in the vertical sagittal plane and myopic in the horizontal plane, and sometimes it is hypermetropic or myopic in both planes, but hypermetropic or myopic to a different degree in each.

The Human Eye Is not a Perfect Dioptric System—1. There is not a perfect centering of the cornea and the lens. The optic

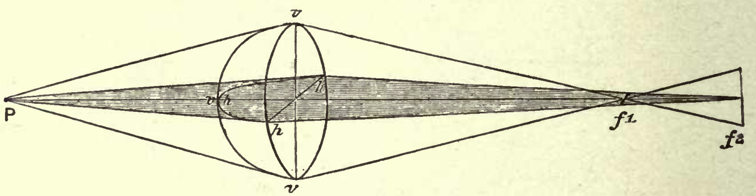


FIG. 17.—ILLUSTRATING THE COURSE OF RAYS REFRACTED DIFFERENTLY IN THE HORIZONTAL AND VERTICAL PLANES (ASTIGMATISM).

axes of the two differ by an angle of 0.3 in the horizontal meridian and 1.30 in the vertical.

2. The optic axis does not strike the center of the fovea centralis, the area of most distinct vision at the posterior pole of the eye. The center of the fovea lies below and to the outside of the posterior pole of the eye.

This visual axis forms an angle of 3.5° in the vertical meridian, and anywhere between 3.5° and 7° in the horizontal meridian. Both these imperfections are too small to create serious defects in vision.

Spherical Aberration—Any perfect lens reflects the rays of light to a greater degree at increasing distances from its center. This circumstance causes the rays of light passing through its periphery being focused in a plane anterior to those passing through the central portions of the lens.

The aberration is corrected in the human eye by (1) the presence of the iris, and (2) the greater degree of curvature which exists in the center of the human lens than at the periphery.

Chromatic Aberration—Rays of white light are composed of many separate rays, each with a different wave length.

Rays of different wave lengths are refracted differently by the periphery of a lens so that there is more or less breaking up of white light by the periphery of a lens into its separate colors.

The iris corrects a certain amount of chromatic aberration. No special optic mechanism corrects chromatic aberration entirely in the human eye.

In fact, chromatic aberration is practically uncorrected in the human eye. The reason that we do not see colored fringes around every object looked at is due to physiological conditions. The eye

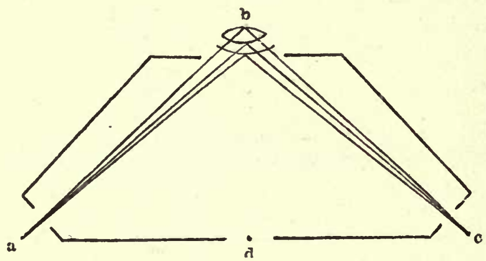


FIG. 18.—DIAGRAM OF PHAKOSCOPE (STARLING).

is far more sensitive to the colors in the middle of the spectrum than to the reds and violets. The excessive sensitiveness to the yellows and greens depresses the neighboring portions of the retina upon which the red and violet fringes fall, and to such a degree that the red and violet fringes are neglected.

Mechanism of Accommodation—Rays of light coming from an object nearer than twenty feet will diverge as they approach the eye.

In order that they may be brought to a focus on the retina, i.e., in order that we may see near objects distinctly, the eye must possess some means of making the curvature of its lens more convex.

The eye accomplishes this by relaxing the tension of the suspensory ligament of the lens. As this ligament exerts its chief force upon the anterior capsule of the lens, the lens, in virtue of its own elasticity, becomes more convex. By means of an instrument called the phakoscope one can see the rays of light which strike the cornea obliquely reflected as three separate images from

the cornea and from the anterior and posterior surfaces of the lens respectively. Only the middle of these, that from the anterior surface of the cornea, changes on accommodation. (Figs. 18, 19.)

During maximum accommodation the radius of the anterior surface of the lens shortens from 10 mm. to 6 mm.

In order to understand the manner in which the curvature of

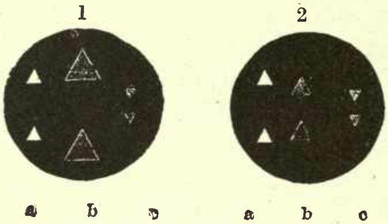


Fig. 19.—Diagram of Reflected Images from Cornea and Lens Surfaces Seen in Phakoscope.

a, from anterior surface of cornea; *b,* from anterior surface of lens; *c,* from posterior surface of lens—1, during accommodation for distance; 2, during accommodation for near objects (Starling).

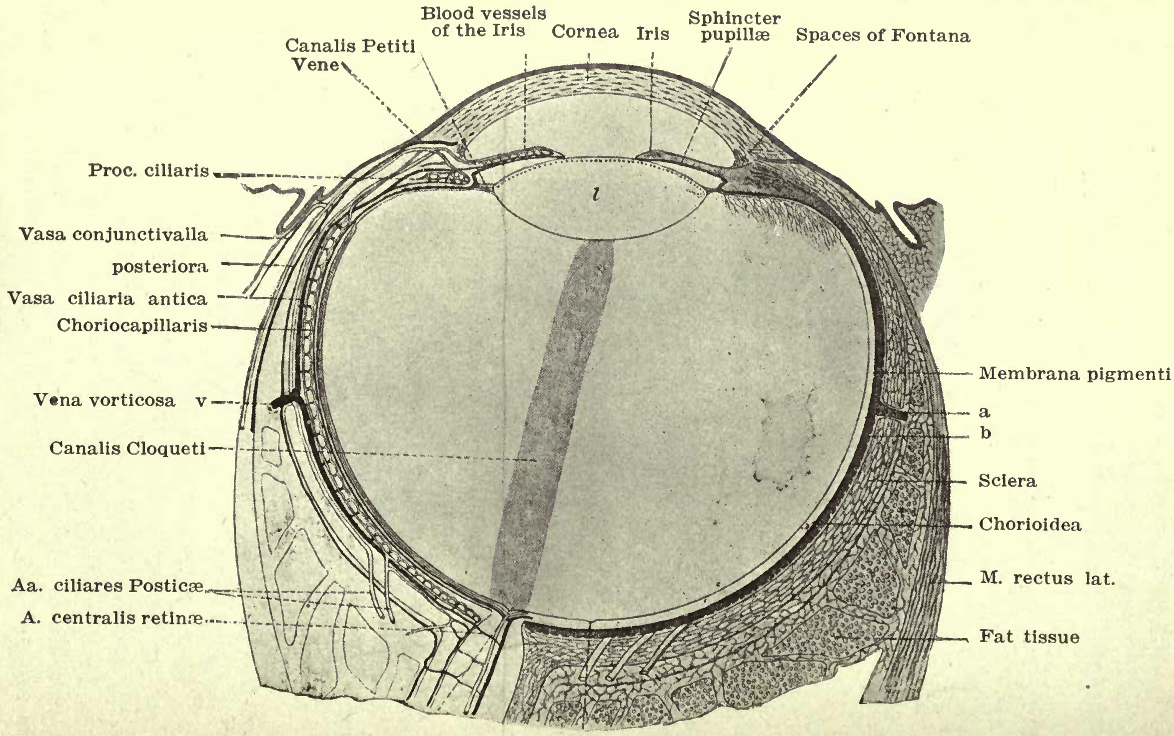
the lens changes during accommodation, it will be necessary to understand the anatomy of the eye.

ANATOMY OF THE EYE

The whole eye is inclosed by a tough white fibrous sac called the sclerotic coat. This is perforated to the inner side of the posterior pole of the eye to allow the passage of the optic nerve. In front it is continuous with the cornea, the clear glassy portion of the front of the eye. (Fig. 20.)

The curvature of the cornea is greater than that of the sclera. The cornea may, therefore, be regarded as closing an anterior opening occupying about two-fifths of the sclerotic sac.

The sclera is lined internally with a connective tissue membrane, the choroid coat, rich in vessels and furnishing the vascular supply to the eye. The internal layers of the choroid are deeply pigmented. In front, just behind the circle of juncture between the cornea and sclera, the choroid terminates in a series of prominences arranged in a circle around the anterior part of the cavity of the eye in this location. These are called the ciliary processes.



Physiological Excavation of the Macula lutea.

FIG. 20.—SCHEMATIC REPRESENTATION OF THE ANATOMY OF THE EYE. *a v*, Vena vorticosa receiving the venous return; *b*, choroid; *l*, lens.

The pigmented layer lines the posterior surface of these processes, and in front of them it is carried further over the continuation of the choroid, which at this place leaves the sclera to form a delicate curtain in front of the lens called the iris.

The pigmented layer of the choroid and its continuation forward over the ciliary processes and surfaces of the iris is composed of a double layer of epithelial cells. From the anterior surface of the iris it becomes continuous (now entirely unpigmented) with the cubical epithelial cells lining the posterior surface of the cornea. These cubical cells, together with the tough elastic membrane beneath them, form the posterior layer of the cornea and is called Descemet's membrane.

This membrane is continuous at the periphery of the cornea with the root of the iris and the anterior termination of the choroid. It is not continuous, however, as a single sheet, but by a series of comb-like processes of fibers which interlace. These interlacing fibers are called the ligamentum pectinatum. Between its fibers are spaces lined with endothelial cells. These spaces are known as the spaces of Fontana and they serve to allow the fluid of the anterior chamber of the eye to come into intimate relation with a venous canal passing in a circle completely around the periphery of the root of the base of the iris immediately outside the spaces of Fontana. This canal is called the canal of Schlemm. Through this canal the fluid of the eyeball passes into the venous system. The lens of the eye is supported by strong fibers passing in a radiating manner from the anterior and posterior surfaces of the lens to the ciliary processes. These fibers form the suspensory ligament of the lens, or the zonula of Zinn. (Fig. 21.) Of these fibers, those of particular importance are those which pass from the anterior surface of the lens to the posterior surface of the ciliary process. Within the ciliary processes are contained three sets of muscular fibers, which together compose the ciliary muscle:

1. A set passing between the corneosclerotic juncture to the anterior end of choroid.

2. A set from the ligamentum pectinatum and canal of Schlemm to the ciliary process.

3. A third set are circular, surrounding the whole of the anterior circle of the eye within the ciliary processes.

A contraction of these three sets of fibers causes a posterior

and internal displacement of the ciliary process and, therefore, a relaxation of the fibers of the suspensory ligament which run to the outer capsule of the lens.

Such a relaxation allows the lens to become more convex in virtue of its own elasticity.

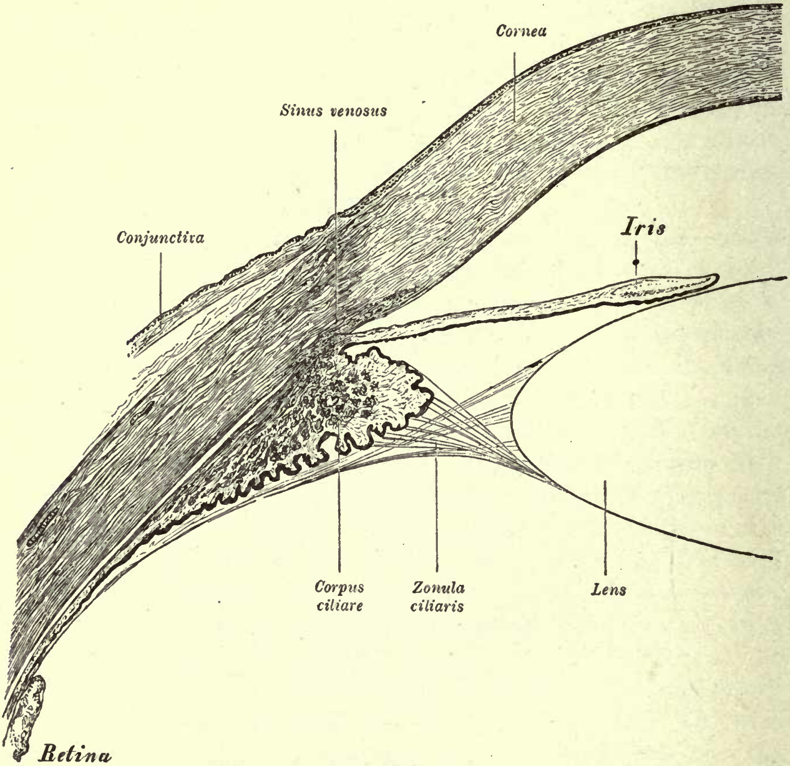


FIG. 21.—CROSS SECTION THROUGH THE ANTERIOR PART OF THE BULB OF THE EYE ENLARGED ABOUT TWELVE TIMES (MERKEL AND KOLLINS).

The following facts demonstrate the relaxation of the suspensory ligament during accommodation:

1. Eserin produces a spasm of accommodation. When instilled into the eye it will produce such a relaxation of the ligament of the lens that the latter will hang loosely suspended.

2. The point of a needle passed into the ciliary processes will

move with them during accommodation in a forward direction indicated by a backward movement of the other end of the needle.

3. With proper illumination the anterior surface of the lens can be seen to approach the cornea during accommodation.

4. The relaxation of the suspensory ligament can be clearly seen in patients with a congenital absence of the iris.

Accommodation, it must not be forgotten, is not accomplished by the same mechanism throughout the vertebrate kingdom.

Functions of the Iris—The iris serves two functions:

1. To shield the eye from excess of light.
2. To diminish spherical aberration.

Contraction of the pupil occurs under two conditions:

1. When light is directed upon the retina.
2. When the eye is directed to a near object.

With moderate degrees of illumination a change in the pupils will not occur in response to a gradual change in the illumination; a pupil contracted to a strong sudden change in illumination will relax somewhat as it becomes accustomed to the light. The range of the change in diameter of the pupil varies from 3.7 mm. to 8 mm.

The response to light occurs after a latent period of 0.4 to 0.5 second, and attains its maximum within 0.1 of a second.

When the eyes are directed to a near object three changes occur simultaneously in them and these three changes are always related:

1. Contraction of ciliary muscle.
2. Convergence of the two eyes.
3. Contraction of the pupils.

The exclusion of an excess of light is essential for the formation of a clear image on the retina. As the amount of light from any object varies inversely as the square of the distance, sufficient light will enter the eye through the contracted pupil for clear inspection of near objects.

In sleep the pupils are contracted.

Dilatation of pupils occurs:

1. When eyes are directed at distant objects.
2. When light is removed.
3. As a reflex response to pain impulses.
4. In emotional conditions.
5. In extreme exhaustion.

The pupil contains two sets of muscular fibers which oppose each other in their action:

1. Sphincter pupili, a circularly disposed bundle of muscular fibers surrounding the opening of the pupils; on contraction they produce diminution in the size of the pupil.

2. Fibers which radiate from the sphincter pupili toward the periphery of the iris. On contraction they produce dilatation of the pupil.

Innervation of the Intrinsic Muscles of the Eye—The ciliary muscle and iris receive nerves from the short and long ciliary nerves. The short ciliary nerves pass to the eye from the lenticular ganglion. The long ciliary nerves pass to the eye from the nasal branch of the ophthalmic division of the 5th.

The short ciliary nerves convey constricting impulses to the ciliary muscles and the sphincter pupili. These impulses reach the lenticular ganglion by means of the 3rd nerve from its nucleus on the floor of the aqueduct of Sylvius. The lenticular ganglion also receive a sympathetic root and a sensory root from the 5th nerve.

The dilator sphincter pupili receives its fibers through the long ciliary nerves, but, though these are branches of the 5th nerve, they contain no fibers of the 5th nerve. The fibers of the long ciliary nerves are all sympathetic fibers which join the 5th nerve at the Gasserian ganglion, and pass to this ganglion from the sympathetic plexus around the carotid artery.

Stimulation of the lenticular ganglion always produces contraction of the pupil and of the ciliary muscle.

Stimulation of the long ciliary nerves of the ophthalmic division of the 5th nerve or of the Gasserian ganglion always causes dilatation of the pupil, but not if the superior cervical sympathetic ganglion has been extirpated.

The Retina—It must not be forgotten that the retina is developed as a protrusion of the brain. It is, therefore, strictly homologous with a lobe of the brain. The original optic vesicle soon becomes inverted so that it resembles a cup with a double-wall posteriorly and a concavity directed forwards. The nervous elements in the layers of the retina must be viewed as true neurons.

Starting from the interior of the eyeball, the following layers compose the retina. (Fig. 22.)

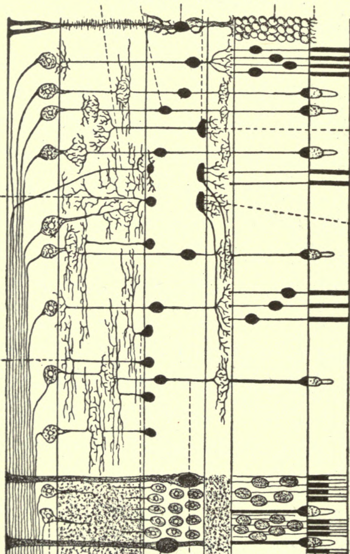


FIG. 22.—SCHEMATIC DIAGRAM OF THE RETINA ACCORDING TO RAMÓN Y CAJAL.
The line *a*, after passing through a Müller's fiber, crosses a bipolar rod-cell, then two bipolar cone-cells, and finally ends in the body of a bipolar cone-cell (Bohm, Davidoff, Huber).

Nerve fiber layer consisting of nerve fibers which have pierced all the coats of the eyeball, including the retina itself and having their medullary sheath, have spread out in a manner to cover uniformly the whole retina and thus reach all the parts. Each individual neuron of the nerve fiber layer is an axis cylinder of a ganglion cell of the next innermost layer of the retina, the ganglion cell layer. These cells are bipolar cells that give off from their opposite end a large dendrite, the terminal branches of which come into relation with the terminal arborization of the axons of bipolar cells of another layer of the retina, more external, the inner nuclear layer.

The interlacing of the dendrites of the ganglion cells with the terminal arborization of the bipolar cells of the inner nuclear layer form another layer between the ganglion cell layer and the inner molecular layer.

The other end of the bipolar cells of the inner nuclear layer ends in a terminal arborization in the outer molecular layer. [illegible] It comes into relation with the terminal arborization of the sensory elements, the rods and cones.

Each rod and cone (Fig. 31) must be considered as a true neuron. The nucleus of the neuron, however, is somewhat displaced from and is anterior to the highly differentiated end of the neuron known as the rod or cone. In fact, the nuclei of the rods and cones form a layer by themselves, the outer nuclear layer. From the small amount of protoplasm surrounding the nucleus, processes pass both externally and internally.

In the case of the rods, the processes passing toward the center of the eye are much more delicate than in the case of the cones. The processes from the opposite end of these nucleated processes, both rods and the cones, end [illegible] in a knob which comes into relation in the outer molecular layer with the terminal arborization of the large bipolar cells of the inner nuclear layer.

The external processes from the nuclei of the rods are thicker and in their expansion which also comes into relation with the terminal branches of the bipolar cells of the inner nuclear layer.

The highly differentiated outer end of the rod and cone ... they each diverge away from the center of the eye [illegible] ... in the case of the rods

Nerve fiber layer consisting of nerve fibers which have pierced all the coats of the eyeball, including the retina itself and, loosing their medullary sheath, have spread out in a manner to cover internally the whole retina and thus reach all its parts. Each individual nerve of the nerve fiber layer is an axis cylinder of a ganglion cell of the next outermost layer of the retina, the ganglion cell layer. These cells are bipolar cells and give off from their opposite end a large dendrite, the terminal branches of which come into relation with the terminal arborization of the axons of bipolar cells of another layer of the retina, more external still the inner nuclear layer.

The intermingling of the dendrites of the ganglion cells and the terminal arborization of the bipolar cells of the inner nuclear layer form another layer between the ganglion cell layer and the inner molecular layer.

The opposite axons of the bipolar cells of the inner nuclear layer end in a terminal arborization in the outer molecular layer. In this layer it comes into relation with the terminal arborization of the sensory elements, the rods and cones.

Each rod and cone (Fig. 23) must be considered as a true neuron. The nucleus of the neuron, however, is separated some distance from and is anterior to the highly differentiated end of the neuron known as the rod or cone. In fact, the nuclei of the rods and cones form a layer by themselves, the outer nuclear layer. From the small amount of protoplasm surrounding this nucleus, processes pass both externally and internally.

In the case of the rods, the processes passing toward the center of the eye are much more delicate than in the case of the cones. The processes from the opposite end of these cells possess little knobs and their distal ends terminate in a knob which comes into relation in the outer molecular layer with the termination of the axons of the bipolar cells of the inner nuclear layer.

The anterior processes from the cone cells are thicker and end in leaf-like expansions which also come into relation with the terminal branches of the bipolar cells of the inner nuclear layer.

The highly differentiated opposite end of the rod and cone cells, that end directed away from the center of the eyeball, is connected by a rather long thin process in the case of the rods,

and a shorter thick cell body in the case of the cones, with the nucleus of these cells in the outer nuclear layer.

The portion of the cell forming the rod and cone must be described separately. Each rod is a long, slender cylindrical body

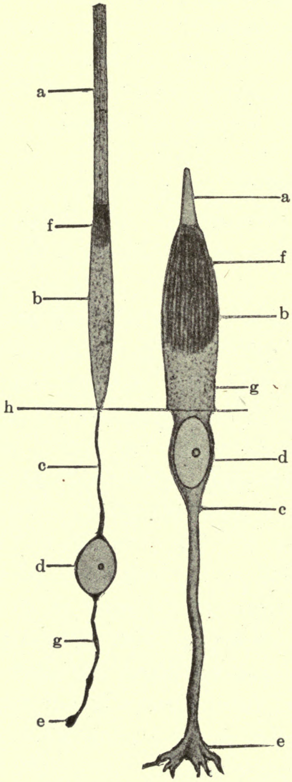


FIG. 23.—A SEMI-SCHEMATIC DRAWING OF A ROD AND CONE OF THE HUMAN RETINA.

a, external process; b, internal limb; c, neck; d, nucleus; e, terminal nodule or arborization with case of the cones; f, ellipsoid; g, varicosities (rods); g, myoid (cones) (von Greef).

containing in an external half, in an eye which has been kept in the dark, a pigment known as the visual purple or rhodopsin. The cones, except for their shape, are much like the rods. They contain a differentiated external and internal half and terminate externally in a conically pointed process.

To sum up, the layers of the retina consist externally of very sensitive elements of two kinds, called rods and cones. The nuclei of these cells form a separate layer, the outer nuclear layer. The impulses from them are picked up in the outer molecular layer by the axons of a bipolar relay cell which transmits the impulse through its opposite process to the external process of another relay cell, the ganglion cell. The axons of these last constitute the optic nerve. The retina, therefore, consists of sensitive peripheral

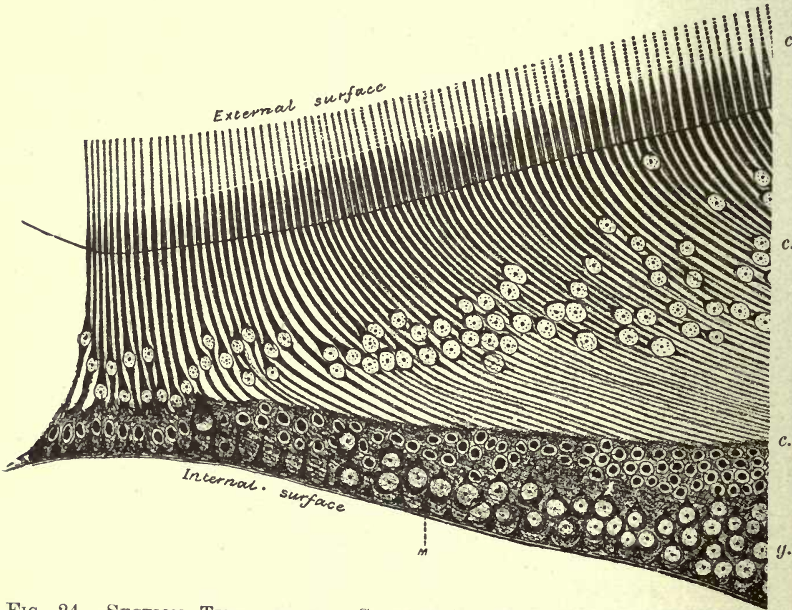


Fig. 24.—Section Through the Central Part of the Fovea Centralis. (From a preparation by C. H. Golding-Bird).

m, bases of Müllerian fibers: *c. g.*, nuclei of inner granules (bipolars); *c. n.*, cone-fiber nuclei; *c.*, cones (Schäfer).

cells and two sets of relay cells. One more kind of cell remains to be described. The retina contains also association cells. They are situated in the inner nuclear layer, i.e., the bipolar cell layer, and are known as the inner and outer horizontal cells, and in the inner molecular layer, where they are called amacrine cells.

Dendrites from these cells break up within the retina itself. They do not form a direct link in the chain from the brain to the visual cells. They must be regarded as association cells. It is

important to remember that there are many more rods and cones than optic nerve fibers. Hence, each ganglion cell receives impulses from several bipolar cells, and therefore from several rods and cones.

At the posterior pole of the eye, external to the entrance of the optic nerve, is situated a small depression, the macula lutea, where vision is most acute. As the center of this spot is approached there is a disappearance of all layers of the retina, except the sentient elements, and these, moreover, consist only of cones. (Fig. 24.)

In the same manner as the periphery of the retina is approached, the cones become less numerous until at the periphery, the ora serrata, only reds exist.

Blind Spot—No sentient elements exist over the entrance of the optic nerve. This constitutes a blind spot in the fundus of the eye. It can always be demonstrated by any individual for himself by simply closing one eye, fixing the gaze of the other eye upon the left of two dots separated from each other 2½ inches, and gradually diminishing the distance between the eyes and dots. The right-handed dot will disappear as soon as the rays from it strike the blind spot.

Visual Purple—The connection of visual purple with vision is an interesting one. Light causes it to disappear, and with such accuracy that actual optograms may be taken by printing through negatives upon the excised retina of rabbits' eyes. It might, therefore, be assumed the disappearance of the visual purple represented a chemical reaction, a substance necessary to vision, and that the reaction products of the purple substance start the impulse along the chain of optic neurons.

The cones, on the other hand, contain no visual purple and they alone are present in the area of most distinct vision. (Fig. 24.) As we shall see presently, the rods probably serve for the transmission of special kinds of visual sensations: namely, those of light and dark as opposed to sensations of color. It is entirely possible that the visual purple may play a part in these special visual impulses.

Electrical Changes—Stimulation of the retina by light is accompanied with a current of action in the same manner as an electrical change accompanies the activity of any neuron.

The galvanometer terminals may be connected with the anterior and posterior surfaces of the eyeball.

Following a flash of light after a very short latent period, .01

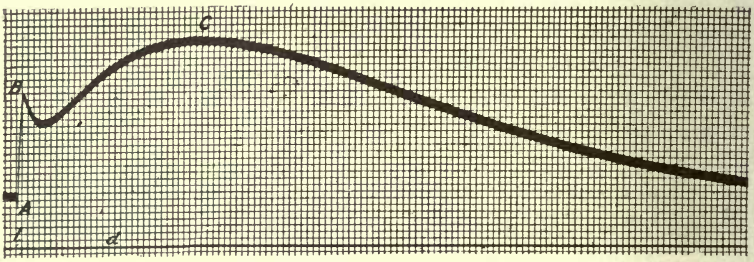


FIG. 25.—THE COMBINED REACTION OF THE THREE SUBSTANCES.

Dark eye: Absc. 1 mm. = 0.5 sec. Ordin. 1 mm. = 10 microvolts; 1 = flash 0.01 sec. of green light; intensity of illumination = 1g; d = darkness (Einthoven and Jolly).

The first change is the drop of the curve at A, produced by activity involving the first color substance in the retina. The second substance acting causes the positive variation indicated by the rise from A to B and the third substance acting causes the second positive rise at C.

of a second, there is a development of the electric change. This change is more complicated than the current of action in muscle or nerve tissue.

There is, first, a negative variation of the resting current, followed by a positive variation, and after this another slow positive

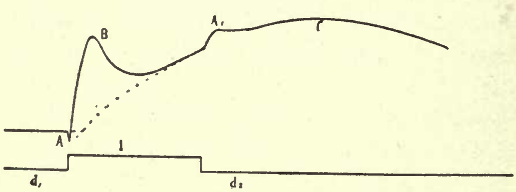


FIG. 26.

variation. (Figs. 25, 26, 27.) The complicated change is explained by the presence of three substances within the retina, each of which possesses its own latent period and electrical curve. (Figs. 28, 29.) It is significant that one of these substances will react toward darkness. We may speak of it as reactive to a flash of darkness.

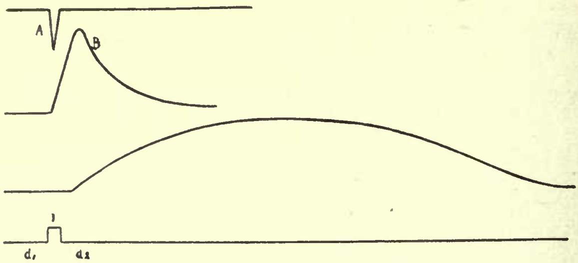


FIG. 27.—A SCHEMATIC REPRESENTATION OF THE RELATIVE HEIGHTS OF THE CURVES AND THE DURATION OF THEIR LATENT PERIODS AND THE RELATION OF THESE PERIODS TO LIGHT AND DARKNESS WHEN COMBINED TOGETHER IN FIG. 26 AND SEPARATELY INDICATED IN FIG. 27.

LIGHT

The stimulus which causes visual sensations are electromagnetic waves of ether propagated through space at a very high velocity. Light travels at the rate of 200,000 miles a second. Only a very small fraction of the total energy of the sun, represented by one over the square of 91,000,000, reaches this earth, and yet this small fraction is the source of all the energy upon the surface of the

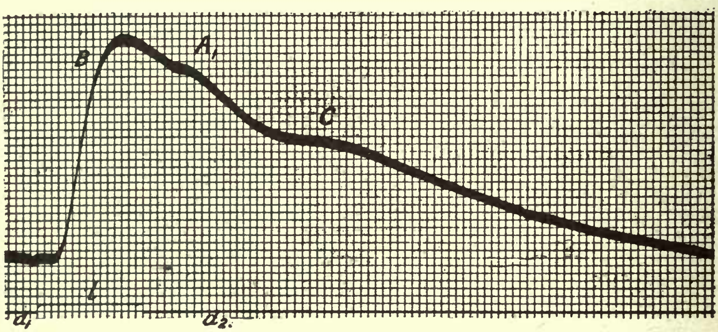


FIG. 28.—A STRONG REACTION OF THE SECOND SUBSTANCE.
Dark eye: Absc. 1 mm. = 0.2 sec. Ordin. 1 mm. = 4 microvolts. 1 = green light. Intensity of illumination = 10-7/g. *l*, light; *d*, darkness (Einthoven and Jolly).

earth. The waves of light are compound waves, made up of many waves, differing from each other in amplitude and rapidity of variation.

By means of the spectrum analysis, waves of light of different

length and rate of oscillation may be separated from each other. By this process of separation the waves must succeed [illegible] with the longest wave length. These will [illegible] and at the portion of the spectrum where they are visible to the eye they appear red. These have a wave-length of 1/39,000 of an inch. At the opposite end of the spectrum come the violet rays with a wave length of 1/57,000 of an inch. In between these the colors of the spectrum occur in the following

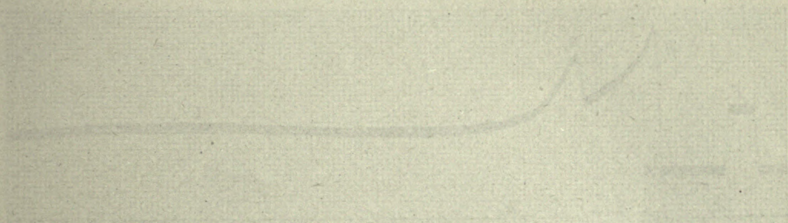


FIG. [illegible]—[illegible]
The [illegible]

order from the red to the violet: orange, yellow, green, blue, and indigo.

A [illegible] have been used to designate the various colored divisions of the spectrum.

Outside the red end of the spectrum rays of light occur which are not visible to the eye. They are called infra-red rays, and carry a very great deal of energy, which may be detected by their heating effect. Beyond the violet end of the spectrum ultra-violet rays also [illegible] may be detected by their chemical action on silver salts. They are therefore called actinic rays. The ultra-violet rays are absorbed to a large extent by the [illegible] of the atmosphere, particularly [illegible] [illegible] rays may be detected in the [illegible]

[illegible] rays are absorbed [illegible] of the [illegible] portion of [illegible]

length and rate of oscillation may be separated from each other. By this process of separation, the waves least refracted are those with the longest wave length. They will occupy one end of the spectrum, and at the portion in the spectrum where they are visible to the eye they appear red. They have a wave length of 1/760,000,000 of a mm. At the opposite end of the spectrum occur the violet rays, with a wave length of 1/397,000,000 of a mm. Between these the colors of the spectrum occur in the following

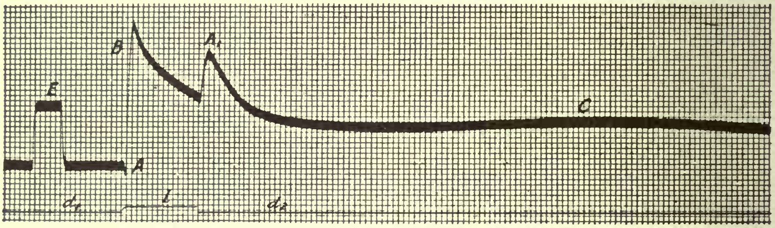


FIG. 29.—A MORE ISOLATED REACTION OF THE THIRD SUBSTANCE.

The reaction is produced by exposing to light an eye which has previously been exposed for a long time to strong light and thereafter darkened for some minutes. The third substance is seen acting feebly at C. Absc. 1 mm. = 0.2 sec. Ordin. 1 mm. = 18 microvolts. *E*, control curve; *l*, light; *d*, darkness (Einthoven and Jolly).

order: from the red to the violet end, orange, yellow, green, blue, and indigo.

Letters from A to H have been used to designate the various colored divisions on the spectrum.

Outside the red end of the spectrum, rays of light occur which are not visible to the eye. They are called ultra-red rays, and possess a very great deal of energy, which may be detected by their warming effect. Beyond the violet end of the spectrum, ultra-violet rays, also imperceptible to the eye, may be detected by their strong action on silver salts. They are, therefore, called actinic rays. The ultra-red and ultra-violet rays are absorbed to a large degree by the constituents of the atmosphere, particularly by water vapors. Very much larger amounts of these ultra-red and violet rays may be detected in the analysis of light at high levels.

Practically all the ultra-violet rays are absorbed by the transparent media of the eyeball, but a considerable portion of the ultra-

red rays arrive at the retina. They are not perceived because they do not stimulate the retina.

The ability of the eye to respond to light, that is, the power of perception of light, is not in proportion to the energy of rays of light.

The most brilliant portions of the spectrum are the central portions, the yellows. They possess a luminosity 1,000 times as great as violet in H and 50 times as great as red in B. Such provision explains how achromatism is in part secured by physiological means.

Weber's law, namely, that the increase of any stimulus neces-

FIG. 30.—THE WEISS-SCHWARZ CARD OF ALTERNATELY ARRANGED BLACK AND WHITE SECTORS.
When rapidly rotated the card appears gray.

sary to produce a perceptible effect is always an increase of a constant proportion to the whole stimulus, is true of the perception of light. In the case of light the ratio is 1/100. We are not able to perceive a difference in luminosity between a luminosity of 99 candlepower and anything below 100. When a momentary flash of light is allowed to fall on the retina, its perception is only fully accomplished after the lapse of a certain amount of time. A certain time is required for the light to reach its maximum effect, after which the effect dies away slowly.

Positive After Images—After the stimulus, therefore, has ceased to act on the retina, perception of light persists. Such after sensations of light are called positive after images. Because of the fact that different colors require different periods of time

for their action on the retina, the period of stimulation of the retina will pass off at different rates of speed for the various rays of which white light is composed. Consequently, when a very bright light is looked at for a short time, the positive after image will pass through a series of colors, at first greenish blue, then violet rose color, and finally orange or green.

It is the persistence of images after the stimuli producing them have been withdrawn, in other words, the positive after images, which accounts for the spokes of a rapidly revolving wheel appearing as though merged into a plane surface. So, rapidly revolving black and white sectors arranged alternately will produce the impression of a uniform gray surface. (Fig. 30.) For complete fusion to take place the period of stimulation plus the period of rest need not be less than .04 of a second. If the illumination is less, this time may be lengthened.

If sectors of a rotating surface are colored, it will be discovered that red will produce the most rapid stimulation of the retina; then come the blues; white and green take the longest time. At certain rates of speed reds and blues alone may be seen. So also the spectrum exposed for only limited moments of time to the eye will appear colorless except for its red end; and alternate black and white sectors rapidly rotated may appear to have colored fringes.

Fatigue Negative After Images—As other excitable tissues, the mechanism involved in the perception of light becomes fatigued by prolonged exposure. Even one-fifth of a second after exposure of the retina to light, the first brilliancy of the illumination diminishes. Fatigue is responsible for the phenomenon connected with the production of a negative after image. If we gaze for a few seconds at a bright light and then look suddenly at a uniformly illuminated surface we will see a dark-colored image with the shape of the bright object first looked at. This is called a negative after image, and is due to fatigue of the portion of the retina upon which the rays from the bright object fell. In virtue of fatigue this portion of the retina responds less readily to the uniformly illuminated surface than the surrounding retina.

Adaptation—The retina possesses the power of adapting itself by a variation in its degree of sensitiveness to different degrees of illumination. All are familiar with the dazzling effects of light

upon an eye which has been in darkness for a long time and also with the ability of the dark adapted eye to see objects which were invisible before the eye became accustomed to darkness. Within 10 minutes after passing into darkness the sensitiveness of one's retina increases 25 fold and 35 fold after two hours. The increased sensitiveness of the retina passes off in five minutes' time

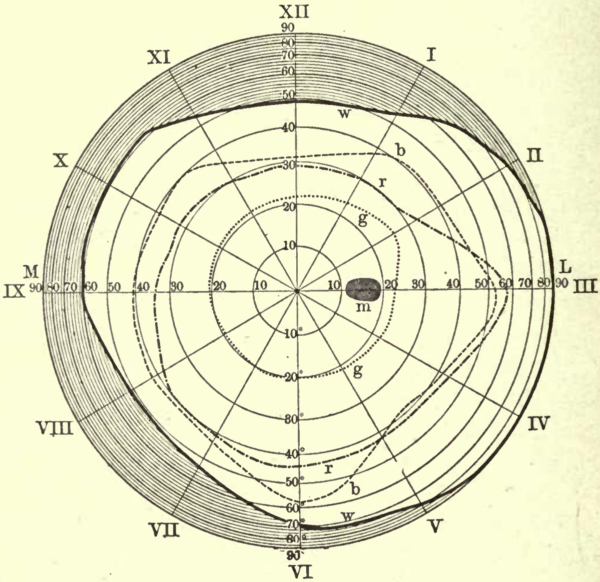


Fig. 31.—A Diagram of the Visual Field of the Left Eye (After Hirschberg).

after exposure to light. Adaptability affects the central fovea far less than the peripheral portion of the retina.

Adaptability of the retina is not exercised at the same rate for all colors. Blues are distinguished most easily in low degrees of illumination and in degrees of illumination in which other colors cannot be seen.

We speak quite correctly of the gray or cold blue of the morning. As the day grows lighter the blue objects or blue flowers in a garden are first visible, and everything has a cold appearance, as if made up of blues, greens and grays.

The red flowers may not be visible at all. A spectrum of colors of a low degree of illumination, when observed by the dark adapted

eye, appears most luminous in the green portion instead of in the yellow, as is the case in the normal eye.

Difference in sensitiveness to colors of the dark adapted eye does not apply to the fovea centralis. In a dark room a small spectrum allowed to fall upon the fovea is seen in its true color value. This is significant in view of the fact that the cones are responsible for color vision, and are alone present at the fovea. It is by rod vision, therefore, that we perceive differences in illumination. The rods are more sensitive to the more refrangible rays and most sensitive to green. (Fig. 31.) Visual purple is doubtless connected with absorption of light by the rods. As regards the absorption of the colors of the spectrum by the retina, particularly by the rod portion of the retina we find that the reds are almost unabsorbed, but that the greens are most absorbed. The retina absorbs just those rays which are most effective in causing the sensation of light by their action on the retina, and does so with the disappearance of the visual purple.

Physiological Explanation of Color Vision—The difference in wave length necessary to produce a difference in the color sensation varies for different portions of the spectrum. For colors in the middle of the spectrum it is .7 millionths mm. to 2.0 millionths mm. The average person will be able to mark off about 18 to 27 color patches in the spectrum, and certain colors, such as purple, which are not seen in the spectrum.

The question next suggests itself, How do we perceive all these colors as different? They are due, of course, to different wave lengths of light, but we cannot assume that there is any difference in the fibers transmitting the color sensations to the brain, nor any difference in the nerve cells of the brain receiving impulses of these nerve fibers, which can account for the different sensation in the perception of green, red or blue independent of the peripheral terminal connections of the nerve fibers in the retina. In other words, the basis of color differentiation must reside in the retina. Certain facts give us a clue as to the nature of this basis.

A combination of red possessing a wave length of 65.6 millionths mm. with yellow having a wave length of 564 will produce orange, and most individuals are familiar with the fact that red and yellow mixed will produce orange. Nevertheless, pure orange of the spectrum possesses a wave length of 608 millionths mm. It is quite evi-

dent, therefore, that it must be a totally different stimulus producing the sensation of orange when caused by the compound wave length of pure red and pure yellow than when produced by pure orange and yet the same sensation of orange is produced in each case. This fact surely indicated that there cannot be a different substance within the retina which is sensitive to each of the colors recognized in the spectrum. The fact is further confirmed by the phenomena of negative after images. The negative after image of any color is that color which will produce white light when mixed with the color which is used for the production of the negative after image. We may say that each negative after image of any colors is its complementary color.

They are as follows: Red, green and blue; orange and blue; bright yellow and blue; yellow and indigo; greenish yellow and violet. If, therefore, any one of these colors produces a negative after image of its own complementary color, it is only necessary to assume the presence of relatively few different sensitive substances in the retina.

The Young-Helmholtz Theory—By the existence in the retina or within each cone of only three such substances—a substance only affected by the red and a substance only affected by green, and another affected only by the violet, we can conceive how any one of these three substances could alone be stimulated by its appropriate colored light or how variations in the impulse could be caused by a proportional stimulation of the three color substances together to such a degree as to correspond with the proportional amount of red, green and violent entering the eye in any one of the colors occurring in the spectrum between the red, green and violet hues. This theory of color vision is called the Young-Helmholtz theory of color vision. (Fig. 32.)

It explains the phenomena of the complementary colors occurring in negative after images well. It explains another phenomenon, color blindness, which also throws light on the physiology of color vision.

All that is necessary to explain color blindness by this theory is to assume the absence of one or other of the three substances sensitive to special color rays.

The normal retina may be said to be trichromatic, while the color-blind eye may be dichromatic or very rarely monochromatic.

Two kinds of dichromatic eyes are known, that in which sensitiveness to red is wanting and that in which sensitiveness to green is lacking. In these eyes only those colors are perceived in which red or green does not occur, either pure or mixed, to form the intervening colors of the spectrum in which red or green plays a part. In the monochromatic eye all three color substances are lacking.

Another theory has been proposed by Hering which explains the facts of color vision quite as well as the Young-Helmholtz

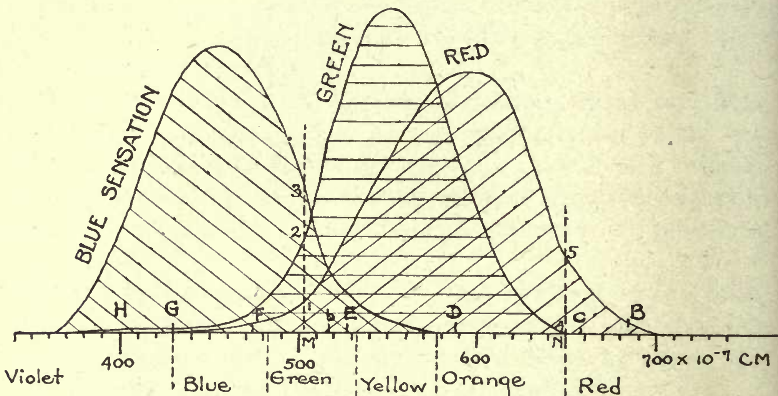


FIG. 32.—DIAGRAM TO ILLUSTRATE THE YOUNG-HELMHOLTZ THEORY OF PERCEPTION OF COLOR BY THE RETINA.

On the base line are given the vibration frequency of the light producing the various colors and the colors produced by the mixture of the three primary colors, blue, green and red, in varying proportions.

theory, and offers certain advantages in the explanation of contrast phenomena, to be dealt with later.

The Hering Theory—Hering assumes that there are three chemical substances in the retina which account for the differences in the stimulation of the retina by colored rays and white and darkness. To two of these substances are given the names of the pairs of complementary colors, namely a red-green substance, a yellow-blue substance. To the substance enabling us to perceive white and black is given the name, white-black substance. Hering assumes further that there are only four primary colors, red, green, yellow and blue, and explains that every ray of a primary color produces either an anabolic or a katabolic change in the color substance. Anabolism in the red-green and yellow-blue sub-

stance respectively would be stimulated only by red and yellow light, and would produce perception of red and yellow. Katabolism of the red-green substances and yellow-blue substances would stimulate the perception of green and blue only.

In the same way anabolism of the white-black substance would produce white light, while katabolism of this same substance would produce black. An equal degree of production of anabolism and katabolism in the red-green and yellow-blue substance would produce white light. The perception of the intervening colors of the spectrum would depend upon varying degrees of uneven excitation of anabolism and katabolism of the complementary color substances.

While both Hering's and Young-Helmholtz's theories offer fairly satisfactory explanations of most of the facts, yet neither of them explain the fact that in every marked degree of color blindness there may be no diminution whatever in the luminosity of any portion of the spectrum.

An individual may not be able to distinguish red, and yet the red of the spectrum will appear illuminated to him. We must, therefore, distinguish between the power of discrimination of colors and the power of appreciating light, and consider that the discrimination of color difference is superadded to and evolved later than the power of appreciating light.

The normal individual will name six colors in the spectrum and mark off about eighteen monochromatic patches in it. A few individuals will add another color called indigo in the spectrum and mark off about twenty-nine patches.

Color blindness will be due to two factors: 1. A shortening of the red or violet end of the spectrum. 2. The absence of the power to discriminate between the colors in the spectrum, though these portions of the spectrum are luminous.

A normal individual will see the red end of the spectrum out as far as a wave length of 760 to 780 millionths mm. The true red-blind person can only see out to 750 millionths mm. They may be detected by testing their powers of discerning colors in which red enters. For instance, rose is a mixture of red and violet. A red-blind person will classify it with the blues, as he only perceives the violet in it. In the same way the true violet-blind individual cannot see the violet end of the spectrum.

In the second class of cases the whole of the spectrum is seen, but there is a deficiency of the power of differentiating color within it. Probably as many as 20 per cent of people have a diminished power of color perception. According to the number of colors which they can see in the spectrum they are named hexachromatic, pentachromatic, tetrachromatic, trichromatic and dichromatic. We may have, for instance, a green-blind individual without shortening of the spectrum.

Contrasts—More light is thrown on the nature of color vision by the study of contrast phenomena. If a gray disc is placed on a red surface and the whole covered with white tissue paper, the gray disc will appear green. The reverse will also be true—a gray disc upon green paper will appear red when the whole is covered with tissue paper.

The negative after image of a red spot on a white background will be green, but surrounding the green spot will be a red-black ground.

Not only, therefore, is the portion of the retina affected upon which the rays fall which come from the colored spot, but also the surrounding retina, although this was subjected to no color stimulation whatever in the conduction of the experiments.

By the Young-Helmholtz theory this fact is difficult to explain unless we consider it a cerebral process. There is no doubt, however, that it is entirely a peripheral affair, and its explanation on this basis is possible by the Hering theory. Hering assumes that the katabolic changes causing the perception of the green color are followed, upon the withdrawal of the green, not only by a stimulation of anabolism leading to a negative after image of red in the portion of the retina upon which the green image fell, but also that the katabolism in one spot of the retina excites anabolism in the neighboring portions and so produces the red field around the central green spot. He names this process "retinal induction."

It is by no means a forced explanation. Many examples exist in the body of similar excitation of assimilative changes excited by dissimilative ones and vice versa. After an inhibition of one reflex by another, the first will reappear with increased force and exercise the same inhibitory or opposite effect on the second. The heart beats with increased force after inhibition through the vagus nerve.

Anabolism within it has been stimulated. The passing off of anelectrotonus is accompanied by increased excitability on the part of a nerve.

The peripheral nature of contrast phenomena may be demonstrated by an experiment in which the contrast color is impressed

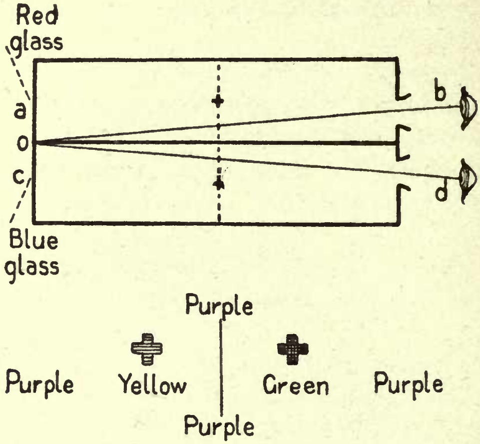


FIG. 33.—In this experiment the crosses indicated on the dotted line are suspended on light gauze, which permits of easily seeing the backgrounds of red by the eye *b*, and of blue by the eye *d*. When, then, both eyes are converged on *o*, the two backgrounds merge and are both purple. The crosses now take the two complementary colors to red and blue, showing that the basis for contrast phenomena is located in the retina of each eye.

upon grey crosses mounted upon a transparent membrane and seen against their complementary colors when provision has been made by the direction of the visual axes for such a fusion of these backgrounds that one background appears and takes the color resulting from the combination of the colors of the two real backgrounds. (Fig. 33.)

PERCEPTION OF VISUAL IMAGES

The same fact is also demonstrated by the greater flickering of the outside completely contrasted portion of a rotating disc compared to the inside or central portion, which is composed also of two colored rings, but each ring only one-half contrasted with its neighboring colors. (Fig. 34.)

Movements of the Eye—Movements of the eye are performed

by six ocular muscles which arise from a tendinous ring around the optic foramen. (Fig. 35.) These muscles rotate the eye around axes which pass through a point almost in the center of the eyeball. Two of the muscles, the external and internal recti, rotate the eye externally and internally around a vertical axis. The superior and inferior recti rotate the eye around a transverse horizontal axis which, however, cuts the sagittal plane of the body at an acute angle. These muscles, therefore, produce a certain amount of convergence.

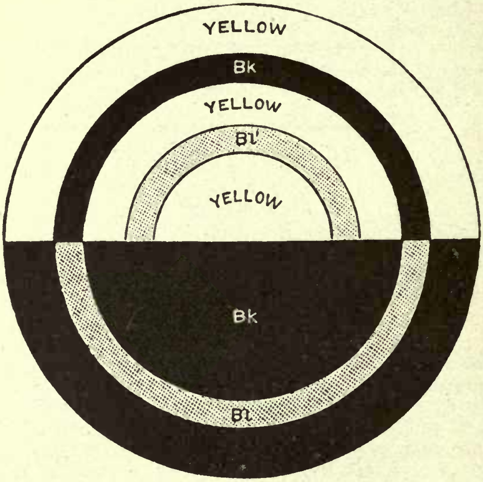


FIG. 34.—A disc so colored that its peripheral half possesses two complete rings, one of which is one-half yellow and one-half black, and the other one-half black and one-half blue, but each ring is completely contrasted with the neighboring color. The central portion of the disc also contains two rings, an external one, half yellow and half black, and an internal one, half blue and half black, but only one-half of each of these rings is completely contrasted with its neighboring colors. When this disc is rotated the peripheral portion flickers longer.

All four of the recti which have been mentioned are inserted into the sclera about 7 mm. behind the corneal margin. The superior oblique and inferior oblique rotate the eye about an anteroposterior horizontal axis which cuts the sagittal plane posteriorly at an acute angle. They both exert their pull from the side of the median plane of the body, and are inserted into the sclera beneath the superior and inferior recti posterior to the middle of the eyeball.

The only two muscles which can produce a normal movement of the eye by acting alone are the external and internal recti. For

all other normal movements of the eyes, elevation and depression, the combined action of several muscles are necessary.

The eyeball rests in the hollow of a pad of fat, which is separated from the sclera by a lymph space contained in a special sac called the capsule of Tenon. It surrounds the tendons of the muscles. The function of the inferior and superior oblique is

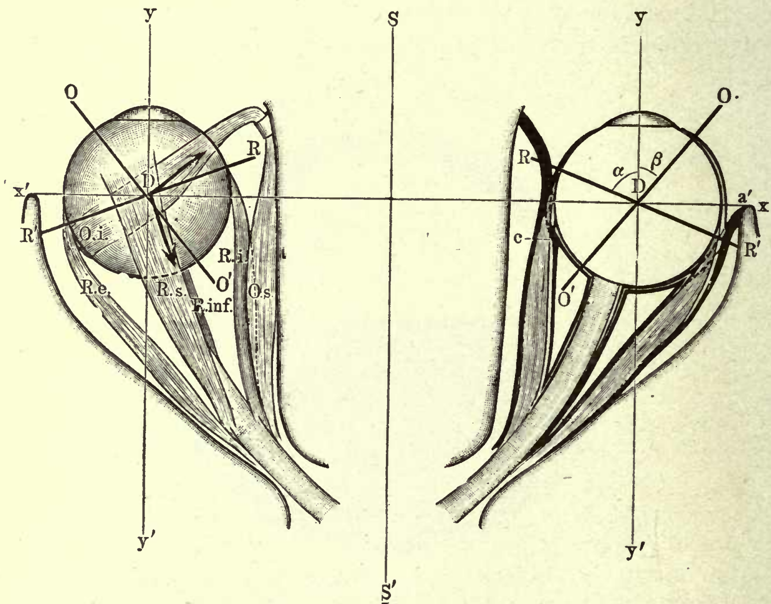


Fig. 35.—The Position of the Rotatory Muscles of the Eye.
Semi-schematic and of natural size. The figure of the left eye shows the direction and attachment of the muscles and the direction of their action. The figure of the right eye shows the relations of the orbital aponeurosis and the bursal sacs of the muscles.

simply to aid the action of the other muscles of the eye. They never act alone, neither does rotation of the eye about an antero-posterior axis ever occur under normally conducted visual acts. A negative after image of a bright line never occupies any other than a vertical position no matter in what direction the eyes may be turned. Acting together, the eyes perform two kinds of movements.

1. The movements of the eyeballs are characterized by a maintenance of parallelism of their visual axes, or

2. By a convergence of the visual axes. In the human being vision is binocular. For binocular vision to be possible the image of the same points in any external object must fall upon homologous but laterally opposite points in the two retinas.

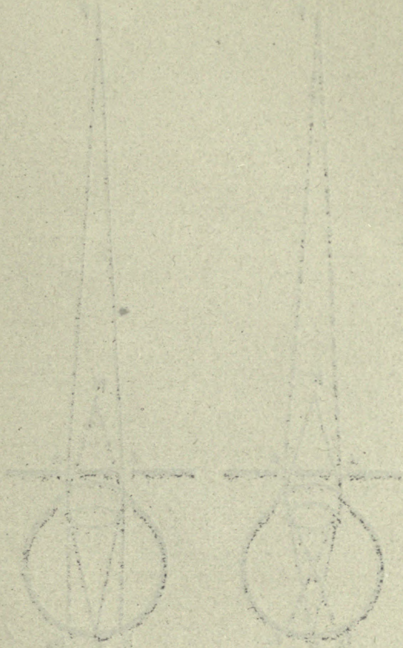
Do the nerves from these laterally opposite but homologous points in the retina pass to the same central nerve cells? They do not.

Single Vision from the Use of the Two Eyes Is a Result of Experience—By experiment it may be shown that the separate elements of single binocular vision are present in both eyes.

Thus, if by an act of convergence a red and blue background are made to fuse, there will at times be a struggle between the color of the two fields so that, while sometimes a purple field as a result of fusion is present, at other times the background will appear sometimes red and sometimes blue. In the same manner, if two fields, one of horizontal lines and the other vertical lines, are converged upon in such a manner that fusion is possible, a cross network will not uniformly be seen but at one time only vertical lines and at another time only horizontal lines.

The Cerebral Part of Vision—All sensory impressions upon the retina are interpreted by the brain entirely as a result of past experience. It is entirely due to this fact that the images upon our retinas which are reversed are always perceived in their true upright position. In other words, we never see at all. All that ever reaches our consciousness through the medium of our eyes are changes in nerve cells situated far back in the occipital region of the cortex. It is, of course, absurd to conceive of the position in the retina from which the impulses start which produce these changes in the central nerve cells as making any difference in the relation of things seen as long as this position remains constant throughout life and thus affords an opportunity for the acquisition of experience in connection with it.

The baby knows nothing of upside down or right and left, only by vainly reaching does it learn where things are. After this experience has been gained, misplacement of the normal relation of one retina to the other will lead to double vision. Such a displacement may be accomplished by pressure on the eyeball, an experiment which can be performed easily by anyone, and one which



will result in a doubling of the object looked at. The same fact is illustrated by the following experiment:

If two holes are pricked in a piece of cardboard nearer to each other than the diameter of the pupil and two points separated by a considerable distance but both in the visual axis are looked at

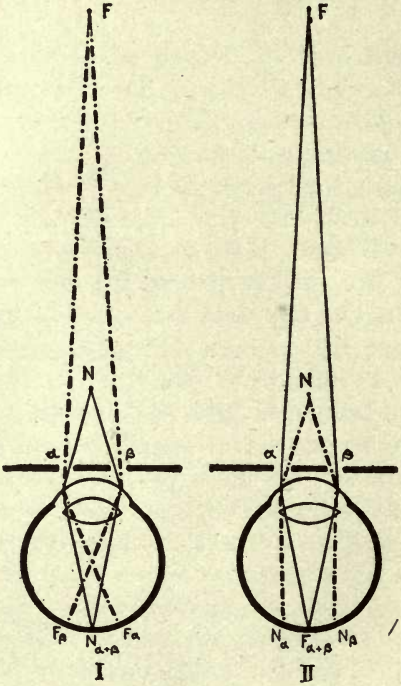


FIG. 36.—DIAGRAM TO ILLUSTRATE SCHEINER'S EXPERIMENT.

F, the far needle; N, the near needle; α and β, two pin-holes in a piece of card. The continuous lines indicate the path of the rays for which the eye is accommodated (Starling).

by one eye through the two holes only the point accommodated for appears single, the image of the other point falls on two places of the retina and appears double (Fig. 36). Our estimation of the size and distance of objects looked at is also a result of experience.

The Factors Participating in the Judgment of Size and Distance—The mind's eye makes use of the following mechanisms and conditions in estimating size and distance:

1. First and most important is convergence: If an object is not

too far away, the degree of muscular effort necessary in order to converge both eyes upon it tells us as accurately as the mathematician's triangle how far away it is. The world appears flat to the individual with one eye.

2. Our judgment of size most frequently depends on our knowledge of how far away the object is. If we know by convergence how far away an object is, the size of the image formed on the retina will give us information upon the size of the object.

3. For distant objects no convergence is necessary, so that the mind's eye must depend upon other conditions for a knowledge of the distance of the objects. Our knowledge of the actual size

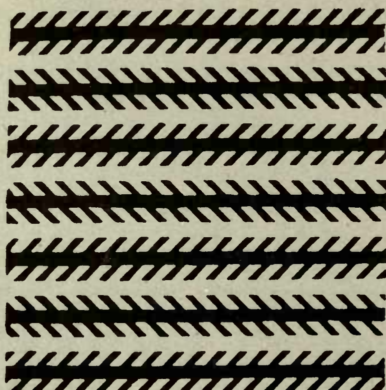


FIG. 37.

of objects in the neighborhood will often aid us in estimating the distance. An after image of the sun will appear of various sizes, according to the varying proximity of the surfaces upon which the after image is formed. The meshes of wire gauze appear large when distant objects are looked at through it, but appear to diminish much in size when the gaze is turned to near objects. The clarity of the atmosphere will have much to do with our judgment of distance and size. On a foggy day a small dog barely seen will be judged to be far off and, until we are close to him, to be the size of a large hound.

4. The muscular effort at accommodation for objects nearer than 20 feet plays a part in our judgment as to their size and distance.

5. More individual effort at movement of the eyeball is required to move the eye across a number of parallel lines than in a direction parallel to their length. For this reason, square space

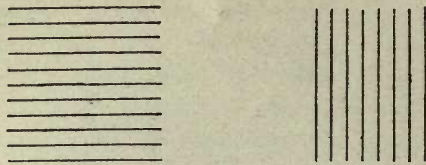


FIG. 38.

occupied by parallel lines appears a little longer in a direction across the lines than corrresponding to their length. For the same reason, straight lines bordered with diagonal branches of equal size will appear crooked. (Fig. 37.)

6. More effort at movement of the eye muscles is required in raising and lowering the eyes than in side-to-side movements, be-

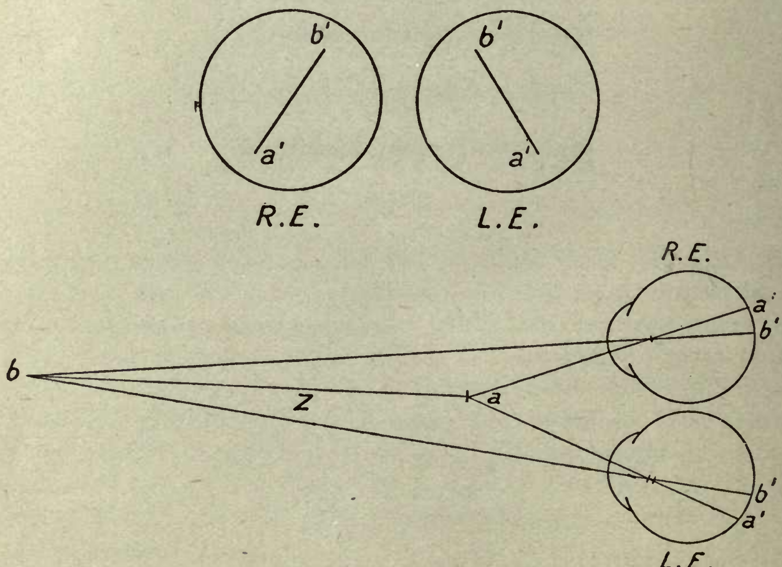


FIG. 39.—The eyes are directed to the point *b*. A thread hung obliquely at *a* under these circumstances gives rise to the images shown in the upper figures—i. e., two images which do not lie on corresponding points. Nevertheless, the thread is seen as single (Starling).

cause in the latter only two muscles are concerned. Therefore, a single line appears longer viewed in a vertical position than when placed horizontally. (Fig. 38.)

7. The mind's eye, however, is so accustomed to depend upon convergence and accommodation for information as to the singleness or double character of any object, and also for its distance and size, that it always waits for the exercise of both convergence and accommodation before forming the judgments. Thus if a thread be only instantaneously illuminated in the dark, no time is allowed for accommodation or convergence, the eyes, which have received the images on the two retinæ in positions which are not homologous,

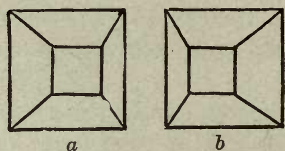


Fig. 40.—The two views of the same objects which fall upon the retina of each eye and which are judged as a result of experience and convergence as coming from the same solid object.

transfer impulses to the brain which are interpreted as coming from one thread. (Fig. 39.)

8. Judgments of solidarity are also dependent upon experience. Any solid object is seen in a different position, each eye viewing it separately. In other words, a differently shaped object is seen by each eye. Nevertheless, the object is always judged as one, because experience has taught us that the image formed in each eye is the proper image to expect from the one object when it is viewed from the two positions of each eye at the same time. The brain, however, is sensitive to the difference in the images falling on homologous parts of each retina and because of the sensitiveness to the different images it is able to judge the object as having three dimensions in space. (Fig. 40.)

The stereoscope fuses two flat pictures of the same view by means of prism-shaped lenses in such a manner that the rays of light coming from each picture falls on the same homologous parts of each retina which would receive the image of a centrally placed

single object looked at from the position of each eye separately. For this reason the stereoscope restores to the fused double picture the impression of solidarity. (Fig. 41.)

Intraocular Pressure—The normal intraocular pressure amounts to 25 mm. of Hg. The fluid maintaining intraocular pressure is renewed chiefly from the vessels in the ciliary processes—1/30 of the fluid passes into the vitreous and leaks away into the

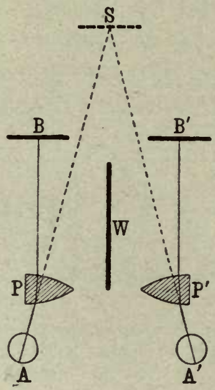


Fig. 41.—Scheme of the Brewster Stereoscope.

The two pictures B B′ are viewed through the lens prisms P and P′. By the refraction of the prisms the two pictures appear to both eyes as merged into one at S. The direction, however, of the optic axes is such that the relation of homologous points of the images on each retina bear the same relation to all other points that they should bear in an object possessing three dimensions represented in only two dimensions in B B′.

plexus of choroid veins. By far the larger amount passes through the fibers of the suspensory ligament of the lens into the posterior chamber and then into the anterior chamber of the eye. From here it passes through the spaces of Fontana and then by Schlemm's canal back into the veins. The resistance of the endothelial lining of the canal of Schlemm is sufficient to maintain an intraocular pressure of 25 mm. of Hg. It is a matter of great importance that this pressure should be accurately maintained and the mechanism by which it is accomplished is a delicate one.

CUTANEOUS SENSIBILITY

The Temperature Sense—By means of nerve endings within the epithelial layers of the skin we may become aware of certain properties of external objects by touching them. These properties are the temperature of external objects and resistance to deformation.

When an attempt is made to investigate the distribution of the cutaneous nerve endings which make possible the appreciation of difference in the temperature and hardness or softness of external objects it is found that there are specific nerve endings for each of these three sensations.

The location of the specific nerve ending may be identified by passing over the skin the end of a small rod or blunt needle which

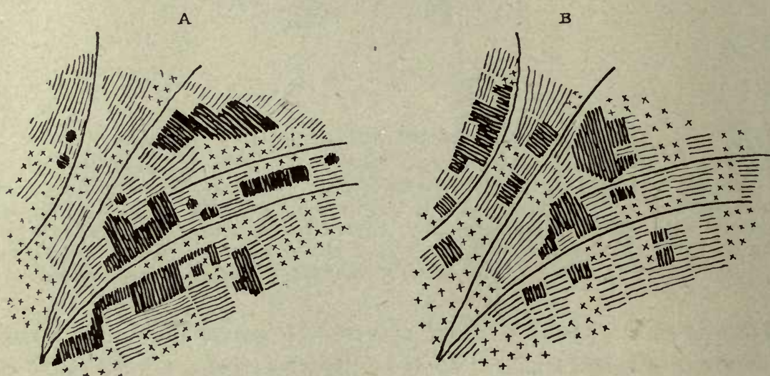


Fig. 42.—The shaded areas indicate the distribution of the temperature sense, which is proportional to the degree of shading.

has been warmed or cooled. If the end of such an instrument is a few degrees cooler than the surface of the skin, only as it passes over the endings of the cold nerve terminals will the cold character of the needle be appreciated. The intervening portions of the skin are insensitive to the cold. In the same manner, if the end of the needle is warmed a few degrees above the temperature of the skin surface, the warmth is only appreciated by isolated spots which are different spots from those sensitive to the cold. (Fig. 42.)

The reason for making use of only slight differences of tem-

perature in searching out the cold and warm nerve terminals is that with greater dryness of temperature it is difficult to avoid confusion of the spots, due to irradiation. The specific function of the hot and cold spots is further emphasized by the possibility of exciting the sensation of cold by bringing a rather hot object into contact with a cold spot, whereas the cold spot is insensitive to a moderately warm object it may be actually excited to produce its own special sensation of cold by a very hot object. Because of this phenomenon, it has been suggested that it might be possible to distinguish between hot and warm sensation and that the former might be due to a simultaneous stimulation of hot and cold spots.

The spots sensitive to cold are far more extensively distributed over the body than the spots sensitive to heat. Both senses, however, are best marked in the nipples, the chest, the nose, the anterior surface of the upper arm, and the anterior surface of the abdomen. It is very much less marked on the face and hands and in general on the exposed parts and is very slight on the mucous membrane.

At the ordinary temperature of the skin, between 27° and 32° C., the acuteness of the temperature sense will permit of the appreciation of differences of temperature of 1/5° C. When the skin is cold or hot, the temperature sense is not nearly so acute.

The temperature sense shows marked degrees of adaptation if the hands are immersed in two vessels containing water differing by a considerable amount in their temperature and then are suddenly immersed in a third vessel containing water at a temperature between that of the hot and cold water. The water in this third vessel will feel hot to the previously cooled hand and cold to the previously heated hand. The possibility of temperature appreciation is not, however, one of mere contrasts, as may be shown by the following experiment: If, for instance, a cold penny is pressed against the forehead and suddenly removed, the sensation of cold will persist although the area pressed upon is becoming warmer.

Touch Sense—By the sense of touch we are able to appreciate differences in the resistance to compression which external objects present to the contact with the surface of the body. Upon investigation, this sense is also found to be dependent upon the presence within the skin of isolated spots sensitive only to pressure. These spots may be identified in much the same manner as the temperature

spots. When the end of a needle comes over a touch spot a definite shooting sensation is perceived which is absent from other spots. If the surface of the skin is gone over with the end of a fine hair or glass fiber attached to a handle so delicate that differences of pressure may be eliminated, the presence of the contact with the skin may not be felt at all except at the touch spots. The touch spots differ in their relative number in different portions of the body. They are very numerous upon the ends of the fingers, where they are seven times as numerous as over the shoulders. Over certain subcutaneous surfaces of bone, as the internal surface of the tibia, as much as 1 cm. may intervene between adjacent touch spots. They are entirely absent from the cornea, the glans penis and the conjunctiva of the upper lid.

The following table represents the minimal effective stimulus per square mm. to the sensation of touch in different portions of the body:

Tongue and nose	2	grams	per	square	mm.
Lips	2.5	"	"	"	"
Finger tip and forehead	3	"	"	"	"
Back of finger	5	"	"	"	"
Palms, arms and thighs	7	"	"	"	"
Forearm	8	"	"	"	"
Back of hand	12	"	"	"	"
Calf, shoulder	16	"	"	"	"
Abdomen	26	"	"	"	"
Outside of thigh	26	"	"	"	"
Shin and sole	28	"	"	"	"
Back of forearm	33	"	"	"	"
Loins	48	"	"	"	"

The closeness of the touch spots determines the sensitiveness of the skin to special discrimination; the fineness, in other words, with which two objects may be appreciated as two and not as one. This power may be tested by pressing upon the skin with the points of a compass approximately at different distances from each other. When so tested the sensitiveness corresponds roughly with the table representing the minimum effective stimulus upon different portions of the body and is as follows:

	Necessary distance between two points on the skin appreciated as double.
Tip of the tongue	1.1 mm.
Volar surface of finger	2.3 mm.
Dorsum of third phalanx	6.8 mm.
Palm of hand	11.3 mm.
Back of hand	31.6 mm.
Back of neck	54.0 mm.
Middle of back, upper arms and thigh	67.1 mm.

These distances may be greatly diminished if individual touch spots are sought out and the distance between the nearest thus tested:

Volar side of finger tips	0.1 mm.
Palm of hand	0.1 mm.
Flexor side of forearm	0.5 mm.
Upper arm	0.6 mm.
Back	0.4 mm.

The rapidity of the response to touch stimuli is very great and is, in fact, of the same order of magnitude, though greater than the response to sound.

For instance, a tuning fork vibrating at a rhythm so great that the sound produced is heard by the ear as a continuous note, if allowed to tap the skin by means of an attached lever will produce the sensation of interrupted taps; and a rotating cogwheel, against the serrations of which the finger is lightly held, will not produce a continuous contact sensation until the individual cogs strike the finger at a more rapid rate than 500 to 600 per second.

The nature of the stimuli appreciated by the touch end organs are such as produce a deformity of the surface of the skin. Mere pressure apart from the production of a change in the relation of the parts of the skin in the area stimulated to the surrounding portions are comparatively, if not entirely, ineffective. For this reason the finger immersed in mercury only feels a constricting ring at the surface of the mercury, where there is the greatest deform-

ity of the surface of the finger, produced by the transition between the heavy mercury and the light air.

Experience has much to do with the interpretation of touch stimuli. We are, for instance, unaccustomed to feel a single solid body at the same moment upon external and internal sides of the fingers, and hence a pea placed upon the contiguous side of the crossed fingers seems to be two peas. Experience with touch stimuli has, moreover, developed the power of the projection of the sense of touch. We are able to tell much about the resistance of external objects by touching them indirectly by means of some other objects, such as a stick or pole, etc., and we are thus able to lengthen or project our sense of touch outside ourselves. Nature, moreover, has made use of this possibility by developing for the advantage of the individual a far richer supply of touch nerve endings in the proximity of the hair follicles. For this reason we appreciate most delicately, in fact, more delicately than by the shaved skin itself, any disturbance of the position of the hairs as may be produced by a breeze or actual contact of the hairs against some insect or foreign body.

Over 9 sq. mm. of the skin from which the hairs had been shaved the minimal effective touch stimulus was 56 mg., whereas on the unshaved skin it was 2 mg.

Pain Sense—The temperature and touch sense constitutes the usual contact stimulus, but quite distinct from it and of tremendous importance to the body is the pain sense. The body must at all locations in which it may come into contact with the outside world be supplied with an adequate means of appreciating the presence of harmful or destructive influences. Separate nerve endings in the skin are set apart for this purpose and they may be identified by piercing the skin gently with a sharp needle. Between such spots no particular pain is felt.

The specific nature of the sense of pain is demonstrated by the fact that excessive stimulation of a touch spot does not produce pain, and moreover by the fact that the pain spots are not sensitive to low grades of stimulation. Further than this, the distribution of the pain sense is different from that of both the temperature and touch sense.

Touch stimuli, for instance, are entirely absent from the cornea, whereas this surface is acutely sensitive to pain.

In certain pathological conditions touch and temperature sensation may be present while the pain sense is abolished. Such a patient is said to be analytic but not anesthetic in the affected areas.

After the division of a sensory nerve to a region of the skin under proper conditions, a regeneration of the nerve may take place with a return of the lost sensations.

The manner in which the sensations return demonstrates the possibility of affecting the fine nerve beneath the surface indirectly through the skin. Such a cutaneous sensitiveness is termed protopathic sensibility.

It will return 7 to 26 weeks after the division of a sensory nerve and is never as acute as the normal sensibility. Thus localization is inaccurate. Only temperatures below 24° C. and above 38° C. can be appreciated as cold or warm, and painful stimuli are more unpleasant. The normal cutaneous sensations or the superficial cutaneous sensations are termed epicritic sensibility. After section of a nerve, it does not return until one or two years have elapsed.

THE SENSE OF TASTE

Sensory impulses of taste are conveyed to the brain by the chorda tympani, the lingual and the glossopharyngeal nerves. All these nerves supply portions of the tongue, the pharynx and the palate, the floor of the mouth and the tonsils and pillars of the fauces. Special connections are made between the termination of these nerves and the surface of the mucous membrane. These connections consist of modifications of the sensory epithelium, termed taste bulbs. The majority of these are situated in the grooves around the circumvallate papillæ; a few, however, are situated in the filiform papillæ and others in the other regions in the distribution of the nerves of taste.

In order to be tasted, a substance must be in solution. Otherwise the sensory epithelium of the taste buds is insensitive to it. The number of primary tastes are few and must be distinguished from flavors. Only tastes may be perceived by means of the sensory epithelium of the tongue. There are four primary taste sensations: bitter, sweet, sour and salty.

Strong evidence exists which demonstrates that different taste bulbs respond at least more sensitively to each of these four primary taste sensations. The back of the tongue, for instance, is more sensitive to bitter and the tip and sides to sweet. (Fig. 43.) Some difference may be detected between even the different circumvallate papillæ. After the application of cocain the power to recognize a

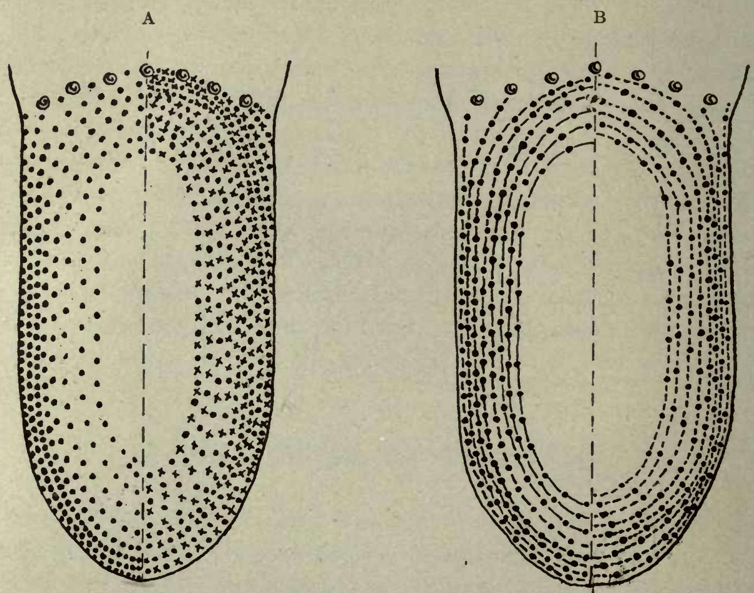


Fig. 43.—Schematic Representation of the Distribution of the Four Fundamental Components of the Sense of Taste upon the Surface of the Tongue.

The distribution of the spots sensitive to sweet is shown in the left half of A. They are more numerous at the tip of the tongue. The distribution of the spots sensitive to bitter is indicated in the right half of A. They are more numerous at the base of the tongue. The distribution of the salt spots is indicated in the left half of B. They are more numerous on the border and tip. The distribution of the spots sensitive to acids is shown in the right half of B. They are most numerous on the borders of the tongue.

bitter taste disappears before power to recognize the sweet and sour tastes which later disappear in the order mentioned. The power to recognize salty tastes is not abolished at all by cocain. After chewing the leaves of the Gymnema Sylvestre the sensations of bitter and sweet are abolished, while acid and salty tastes remain.

Many acid substances, in addition to stimulating the taste bulbs,

produce an astringent action on the nerve endings. Such an action must also be distinguished from acid tastes. The character of the sensations of taste are profoundly modified by a mixture of substances normally stimulating very different taste sensations. Thus a mixture of lemon and sugar produces a very pleasant taste in which the components can be easily distinguished.

In addition to the primary tastes, many substances when taken into the mouth cause flavors. The number of flavors are very numerous. Their perception is not accomplished by the taste buds at all, but by the nerves of smell. Without the sense of smell the enjoyment of things eaten amounts to very little.

THE SENSE OF SMELL

In man the sense of smell is vestigial. Among the animals, as for instance the dog, the sense of smell is of very great importance and enters largely into many of his concepts, so that by its association much of his thought is made possible. The end organs of smell consist of a layer of columnar epithelium resting on several layers of nuclei. The latter are the nuclei of spindle cells, really a bipolar afferent neuron, with one long process reaching up between the columnar cells and the opposite process extending as a non-medullated nerve fiber through the grooves on the cribriform plate of the ethmoid to the olfactory lobes, where their terminal arborization ends by intermingling with the arborization of the peripheral process of the mitral cells. The columnar cells constitute the olfactory sensory epithelium and cover the superior and middle turbinates and the upper part of the nasal septum. In contrast to the epithelium over the lower part of the septum and the inferior turbinated bone, it is not ciliated as the latter and possesses a yellow color.

The upper portion of the nasal cavity is not reached during ordinary quiet respiration, hence for the maximum use of the sense of smell forced aeration of the region of the superior turbinated bone, as in the act of sniffing, is necessary.

All odorous substances must be in a gaseous form and the majority are gases with large molecules. On this account they diffuse slowly, and this explains why smells tend to hang around objects.

Inasmuch as the olfactory membrane is moist, it is necessary for the odorous particles to be soluble and dissolved in this fluid before they are able to excite the olfactory epithelium. In the case of aquatic animals the odorous particles certainly excite the olfactory epithelium in solution, for these animals are able to project a chemical discrimination which is actually the sense of smell.

Moreover, even in man it has been claimed that odorous particles dissolved in saline solution may be detected by the olfactory epithelium when the nasal cavity is filled with this fluid.

As with the sense of taste, pungent odors, as ammonia producing an astringent or inflammatory effect, stimulating the nerves of common sensibility, must be distinguished from odorous particles capable of stimulating the olfactory epithelium. Smells have never been satisfactorily classified. The olfactory epithelium, however, probably possesses specific sensitiveness in its relation to various odors. Some individuals, for instance, have no power of distinguishing odors perceptible to other individuals. When the olfactory epithelium is fatigued for one odor, it is still as sensitive for others. It is possible to mix certain odorous substances in a manner to absolutely nullify the action of each upon the olfactory epithelium. Four grams of iodoform and 200 grams of Peruvian balsam is odorless, and both substances may also be unperceived if presented separately to the nostrils.

QUESTIONS AND ANSWERS

Page 4

Q. What are auditory stimuli?
A. Wave-like vibrations of the molecules of the air.

Q. What is the difference between a musical tone and a noise?
A. A noise is a series of irregular vibrations in the air. A musical tone is a series of vibrations which repeat each other in a more or less regular or rhythmical manner.

Q. What are the characters which distinguish sounds and musical tones, and define each character?
A. See text.

Page 10

Q. Define consonance and dissonance.
A. These words define the reinforcing or interfering effect of the fundamental and overtones of two musical notes when sounded together.

Q. Define a musical note.
A. Wave-like vibrations of the air produced by the compound effect on the air of some fundamental tone and its secondary or overtone vibrations.

Page 14

Q. Describe the anatomy of the ear. See 765 Potter
A. See text.

Q. Name the portions of the transmitting mechanism of sound from the external ear to the auditory epithelium.
A. 1. External auditory meatus.
2. Tympanic membrane.
3. The chain of ossicles.
4. The fenestra ovalis.
5. The vestibule.
6. The scala vestibuli.
7. The scala media.
8. The fibers of the basilar membrane.
9. The membrana tectoria.
10. The hairs of the auditory epithelium.

Page 26

Q. Describe the organ of Corti and tissues which have a functional relation to it.
A. These include the basilar membrane, the membranæ reticularis and tectoria. See text.

Page 28

Q. What is the physical basis of the power to discriminate pitch?

A. The different length of the fibers of the basilar membrane, which makes possible the throwing into strong vibration a single fiber for each discernible pitch of sound. The vibrating fiber agitates the hairs of the auditory epithelium, of the portion of the organ of Corti, which is in relation to it and the membrana tectoria against each other.

Page 30

Q. Describe the anatomy of the vestibule and the semicircular canals.
A. See text.

Page 36

Q. What are the sensitive elements of the saccule, utricle and semicircular canals?

A. The hair cells of the maculæ acusticæ in the utricle and saccule and in the ampullæ of the semicircular canals.

Page 38

Q. To what stimuli are the sensitive elements of the utricle and saccule and semicircular canals sensitive?

A. In the saccule and utricle more particularly to changes in the direction of the gravity of the otoliths. In the semicircular canals to changes in the direction of the currents of endolymph. The whole organ constituting the organ of equilibrium, and enabling the animal to appreciate changes in the position of the center of gravity.

Page 40

Q. What two provisions are essential for the perception of sight, and what does each accomplish?

A. An epithelial surface sensitive to light and a dioptric mechanism so focusing light waves that images of external objects looked at are reproduced upon the retina.

Page 42

Q. What is meant by the nodal point of the eye?

A. The center of hypothetical curvature representing the combined refractive power of the different refractive media of the eye.

Q. Construct the path of two rays through the eye from the extreme ends of some external object.

A. See text.

Page 48

Q. In what particulars is the human eye an imperfect dioptric mechanism, and define the meaning of each deviation and the method of its partial correction?

A. 1. The optic axis and the visual axis do not quite correspond.
2. Spherical aberration, due to greater refraction of the periphery of a lens, is not perfectly corrected, though it is corrected by both the presence of the iris and a difference in the degree of curvature of the periphery and center of the lens.
3. Chromatic aberration, the difference in the degree of refraction of the different wave lengths by the periphery of the lens, is uncorrected except by physiological means.

Page 50

Q. What is accommodation, and explain its mechanism?

A. Accommodation is that function of the eye by which it adjusts its dioptric mechanism so that near or far objects are brought to a focus on the retina. It is accomplished by the ciliary muscle, which, upon contraction, relaxes the anterior fibers of the suspensory ligament and allows the lens, in virtue of its elasticity, to become more convex.

Page 52

Q. Describe the anatomy of the eye and draw a diagram of the human eye, inserting and naming the different important structures and tissues of the eye.

A. See Fig. 20.

Page 60

Q. What are the functions of the iris?

A. See text.

To shield eye from excess light Diminish spherical aberration

Page 66

Q. Describe the sentient cells of the retina, their position in the retina and how many units constitute the chain of neurons in the retina, and, in a general way, the layers of the retina.

A. The sentient cells are the rods and cones. Each are nerve cells with an axon which comes into relation with another neuron in a more anterior layer of the retina, the bipolar cell layer. The anterior axons of these come into relation with the nerve cells of the ganglion cell layer of which axons from the fibers of the optic nerve. The posterior half of each rod and cone is most highly specialized, and, in case of rods, is thin and contains a pigment, the visual purple. The rods and cones are set closely together in the most posterior layer of the retina, the cones being progressively more numerous toward the center of the retina. They constitute the first link of the three forming the chain of neurons of the retina, the layers of which simply consist of the bodies of these cells, separated by intervening layers, composed of the intermingling fibers of their axons.

Page 76

Q. Describe the physical properties of light of physiological interest.

A. See text.

Page 80

Q. What portions of the spectrum are most brilliant to the eye?

A. The yellows. Perception is not proportional to the energy of the ray. It corresponds to Weber's law and possesses a certain latent period.

Q. What are positive after images and some of the phenomena which they give rise to?

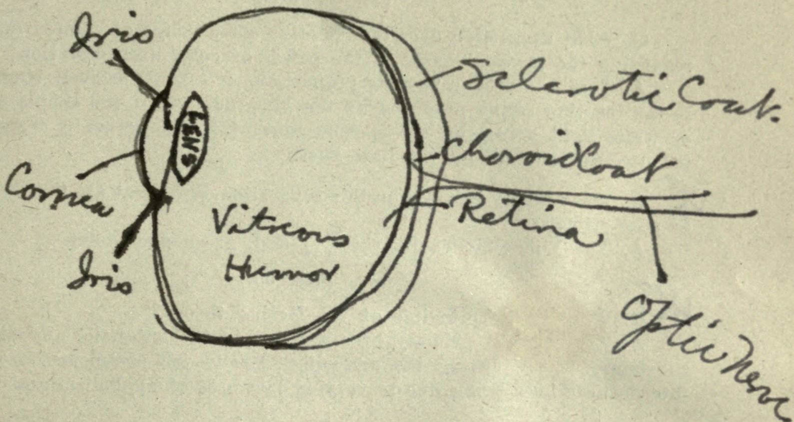
A. See text.

Page 82

Q. What is a negative after image, and to what is it due?

A. See text.

Q. How does adaptation modify the perception of light in different degrees of illumination by the retina?


Iris
LENS
Sclerotic Coat.
Choroid Coat
Cornea
Retina
Vitreous Humor
Iris
Optic Nerve

A. Adaptation decreases sensitiveness to light, the dark adapted eye being far more sensitive. Except at the fovea centrales there is a difference in the intensity of illumination necessary for the perception of certain colors which is different for different colors.

Page 88

Q. What suggestion does the negative after image of colored light furnish regarding the physical basis of the power of color discrimination?

A. That mixtures in varying proportions of a few relatively simple changes in the reacting retina produced by the same number of the simple components of white light acting on the specific element in the retina is responsible for the perception of all intermediate hues.

Q. What theory is based on this suggestion, and what are the three primary or pure stimuli?

A. The Young-Helmholtz theory. Red, green and violet.

Page 90

Q. What is the principle of the Hering theory?

A. That certain primary hues are due to the katabolic anabolism of the substance, which, during the anabolism, excite the complementary hues, the intermediate hues being due to varying mixtures of anabolism and katabolism.

Page 94

Q. Explain the meaning of contrast phenomena, and are they in accord with Hering's theory of color perception? They are in accord

A. Contrast phenomena are the perceptions of the complementary colors by that portion of the retina fatigued or previously used in the perception of the color to which the contrast color is complementary. They are in accord with the Hering theory better than with the Young-Helmholtz theory, as numerous illustrations exist in the body of the stimulation of anabolism by a previous period of katabolism or of katabolism by a previous period of anabolism.

Page 104

Q. What are the factors concerned in the judgment of size, distance and solidarity?

A. 1. The effort of convergence required to see singly.
   2. Upon comparison with the size of other known objects near the one viewed.
   3. Effort of accommodation required to see it distinctly.
   4. Upon the experience of the different shape of a known solid object as viewed by the two eyes in their different positions in the head.

Page 114

Q. What cutaneous sensibilities are appreciated by special nerve endings?

A. 1. The sense of cold.
   2. The sense of heat.
   3. The sense of pain.
   4. The sense of touch.

Page 116

Q. How uniformly are the nerve endings of cutaneous sensibility distributed?

A. Very unevenly. Wherever they are most numerous for any particular sensation that sensation is most keenly appreciated. In general cutaneous sensation is most marked on lips, tongue and fingers for touch, and on nipples, chest, abdomen and arm for temperature sense.

Page 118

Q. What are some of the physiological characteristics of cutaneous sensibility?

A. 1. Uneven distribution over the body.
2. Show much adaptation.
3. Depend upon cerebral interpretation to a large degree.

Page 122

Q. What are some of the characteristics of the pain sense?

A. Its failure to correspond in its topography to the touch sense.

Page 124

Q. What is the difference between protopathic and epicretic cutaneous sensibility?

A. See text.

Q. How many primary tastes are there, and what are they?

A. Four: bitter, sweet, salt and acid.

Page 126

Q. What is the sensitive element of each individual taste and how are the taste bulbs distributed on the tongue?

A. A separate taste bulb for each taste, the back of the tongue being more sensitive to bitter and the sides and tip to sweet.

Page 128

Q. To what is the perception of flavor due?

A. To the sense of smell.

Q. Describe the minute anatomy of the peripheral portion of the olfactory mechanism.

A. See text.

Page 130

Q. Does the olfactory mucous membrane possess a specific sensitiveness to certain odors, and what is the evidence concerning this possibility?

A. See text. Yes —